

# Review of Australian Cave Guano Ecosystems with a Checklist of Guano Invertebrates

TIMOTHY MOULDS

Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Sciences, University of Adelaide, North Terrace, Adelaide 5005.  
timothy.moulds@adelaide.edu.au

Moulds, T. (2004). Review of Australian cave guano ecosystems with a checklist of guano invertebrates. *Proceedings of the Linnean Society of New South Wales* 125, 1-42.

This work provides a check-list of all invertebrate species known, or believed to be, associated with cave guano in Australia. A total of 240 species in 121 families, representing 25 orders is listed. These species inhabit 60 karst areas in all mainland states of Australia and Christmas Island (Indian Ocean). Comprehensive assessment of all available records (published and in collections) show that the distribution of several species is more extensive than previously believed. It is unknown whether this is because of inadequate identification of specimens, poorly defined taxonomy or unrecognised intra-species variation due to a lack of specimens. Twenty species from five orders show restricted distributions and guano dependence, although endemic status can not yet be assigned. Amongst these species, eight pseudoscorpions and eight Coleoptera are distributed across several mainland states and Christmas Island.

Manuscript received 2 July 2003, accepted for publication 22 October 2003.

Keywords: Arthropoda, Australia, biospeleology, cave, checklist, ecosystem, guano, invertebrate.

## INTRODUCTION

Australian cave guano ecosystems are poorly known with only a few communities studied in detail (e.g. Richards 1971; Harris 1973; Bellati et al. 2003). Previous studies concerned with the terrestrial cavernicolous fauna of Australia have mentioned species associated with guano, but have provided little in the way of detail with regard to the ecology of specialised guano communities and species. This paper seeks to synthesise the knowledge of guano ecosystems and communities in Australian caves. A review of guano ecosystems and habitats precedes a checklist of all species known to be associated with Australian cave guano deposits.

Populations of cavernicolous animals are usually small because of limited food supplies. However, caves containing guano differ fundamentally because there is a virtually unlimited food supply, commonly resulting in large animal populations. Guano in caves is deposited by bats, birds, orthopterans (crickets and grasshoppers), and small mammals, with each type of guano sustaining a unique assemblage of taxa. Guano deposits are extremely variable, unlike other cave habitats, and consist of numerous micro-

habitats differentiated by fluctuating temperature, moisture, and pH. Guano ecosystems contain obligate guano-dwelling organisms (guanobites), opportunistic guano-dwelling animals (guanophiles), and transient guano-using animals (guanoxenes) (Gnaspini and Trajano 2000). The basis for many guano ecosystems is the numerous species of fungi and bacteria that can grow on guano, even in complete darkness.

### Cave food sources

Cavernicolous populations are dependant for their survival upon energy inputs into cave systems. These inputs can vary widely, with availability of food usually being the primary limiting factor (Peck 1976). Inflowing streams and periodic floodwaters introduce significant amounts of zooplankton, accidentals, and organic debris that, for many cave ecosystems, represent the main energy inputs (Peck and Christiansen 1990; Humphreys 1991). Tree roots penetrating the roofs and walls are another important energy source found commonly in tropical caves and lava tubes (Hoch 1988; Hoch and Howarth 1999). Dead animals can be a source of food for scavengers near cave entrances (Richards 1971). Accidentals wandering in from cave entrances also provide a food

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

source, although this is generally periodic in nature and inconsistent in quantity.

For the most part cave environments are generally depauperate in food and consequently are sparsely populated with cavernicolous animals. However, caves containing guano deposits differ substantially because they have a virtually unlimited food supply. When present, guano from bats, birds, and Orthoptera (crickets and grasshoppers) generally forms the major energy source (Park and Barr 1961; Poulson 1972; Martin 1977), with large, varied and unique ecosystems often revolving around such deposits.

### SOURCES AND DIVERSITY OF CAVE GUANO

Cave guano deposits from specific sources can each possess a unique assemblage of taxa (Horst 1972; Poulson 1972). Throughout the world's biogeographic provinces different taxa are responsible for being the most important guano producers. The most widespread and common guano is that produced by bats and these deposits are generally the largest in volume. The spatial and temporal deposition of bat guano differs from tropical to temperate caves. Cave-dwelling bats in temperate regions show an annual cycle of occupancy over summer months when pups are born, before colonies disperse to cooler, wintering caves where they enter torpor. This annual cycle results in large amounts of guano deposited over summer months and then a cessation of guano input for approximately seven months. In contrast, tropical caves generally show constant bat occupancy rather than an annual cycle and less congregation of individuals due to warmer ambient temperatures. Gnaspini and Trajano (2000) note that many bat populations in tropical Brazil are commonly nomadic, resulting in roaming colonies varying their location in an irregular and non-seasonal fashion. This results in non-continuous deposition. The diet of bats (either haematophagous, insectivorous, frugivorous, or nectarivorous) also influences the composition of guano piles and hence the associated guanophilic communities (Gnaspini 1992; Ferreira and Martins 1998, 1999). Large populations of the common vampire bat (*Desmodus rotundus* Geoffroy) predominate in Brazilian karst near inhabited areas, due to large numbers of domestic livestock resulting in haematophagous guano deposits. Guano from non-haematophagous bats is absent, or greatly reduced as vampire bats exclude other bat species, thus changing the guanophilic communities present.

Birds are common guano producers in the northern parts of South America, the Caribbean and

tropical caves of south-east Asia. Cave-dwelling birds nest in the dark zone, providing an important energy resource for many cavernicolous animals. Cave-dwelling birds in South American and Caribbean caves include guácharos (*Steatornis caripensis* Humboldt) (Snow 1975; Gnaspini and Trajano 2000). This bird discards palm seeds, sometimes with flesh still attached, and deposit droppings in caves, thus providing a wide range of organic matter for cavernicolous animals. Because of the presence of discarded seeds, some taxa associated with seeds and detritus, such as lygaeid bugs are found only in guano of this type. Swiftlets (*Aerodramus* spp) nest in the entrance and dark zones of tropical caves in south-east Asia, northern Australia and the Pacific and are insectivorous (Medway 1962). These birds also support a range of guanophilic taxa in the caves of Christmas Island (Humphreys and Eberhard 2001). Richards (1971) reported that droppings from several species of birds nesting in the entrance zone of Nullarbor Plain caves support a wide variety of cavernicolous animals.

Rhaphidophorid crickets are often important producers of guano in temperate caves such as those of the Nullarbor Plain (Richards 1971). The sometimes large populations of these crickets can accumulate sizeable guano deposits in caves. These deposits are important as few other food sources exist in areas such as the Nullarbor Plain because the low mean rainfall limits organic flood debris and bat populations are generally small. Rhaphidophorid guano is also utilised in Mammoth Cave, Kentucky, where it is widely dispersed through the cave system (Howarth 1983).

Small mammals are often significant guano producers in temperate zones of North America. The guano of porcupines (*Erethizon dorsatum* L.) is reported by Calder (1965) to support a community of collembolans and mites active throughout the year in Frenchman's Cave (Hants County, Nova Scotia, Canada). Cave rats (*Neotoma* spp), navigate using urine trails (Howarth 1983). Although common in the caves of the Canadian Rockies and Vancouver Island, their faeces are mostly unusable as a food source due to the high ammonia content from systematic urination at these sites (Trapani 1997).

### GUANO ECOSYSTEMS AND FOOD WEBS

Guanobites are animals that require the presence of guano for survival. They will only feed on guano and will not use other food sources within caves. Although guanobitic species are occasionally found on other substrates in caves as they move between discontinuous guano deposits, they do not feed

or reproduce on these substrates (Gnaspini and Trajano 2000). When guano deposition is seasonal (e.g. bat maternity caves), guanobites will commonly become quiescent until bats return and restore fresh guano input. Other guanobite populations crash when guano input ceases and then quickly reproduce when guano input recommences.

Guanophiles use guano resources opportunistically and are able to complete their entire life cycle using the guano substrate. Guanophiles will however utilise other cave food resources when available and do not have to rely upon guano to feed or reproduce. Abundance of guanophilic animals will decrease if fresh guano is not available, simply due to food limitation, but individuals will attempt to exploit other food resources to survive until fresh guano is available. Troglobites and trogloniles that have a generalist role in epigeal ecosystems are classified as guanophiles if they utilise guano when available, even though they are capable of surviving subterranean habitats without this resource.

Guanoxenes will exploit a guano resource for feeding or reproduction but require other substrates within a cave to complete their life cycle (Gnaspini and Trajano 2000). Guanoxenes can be either troglobites, trogloniles or troglonoxenes (Gnaspini and Trajano 2000).

The cyclical nature of many guano deposits resulting from the annual breeding cycle of bats, leads to a similar cycle in arthropod abundances. Low population numbers of many species reflect changes in micro-habitat conditions resulting from the cessation of fresh guano deposition and lower air and guano temperatures. Guano communities decrease in numbers as many species stop breeding until the food supply (i.e. fresh guano) is restored. This has been observed in the mite *Uroobovella coprophila* Womersley, which is quiescent during winter months in Carrai Bat Cave, northern New South Wales (Harris 1971).

Arthropods in guano communities feed either directly on guano or fungus growing on guano deposits and these in turn support a number of predators scavengers and omnivores (Gillieson 1997). Generalised guano food webs have a guano source directly supporting a range of guanivores including Phoridae (Diptera), Anobiidae (Coleoptera), Tineidae (Lepidoptera), Collembola and mesostigmatid mites (Acarina). Predators that prey upon these consumers include spiders, pseudoscorpions, beetles and opiliones. Specialised parasites and parasitoids are also active in many guano ecosystems. Braconid wasps (Hymenoptera) are found in many Australian guano caves and parasitise the larvae of *Monopis* spp (Lepidoptera: Tineidae). The larvae of the guanobite

*Derolathrus* sp. (Coleoptera: Jacobsoniidae) are parasitised by small myrmecid wasps (Hymenoptera). Parasitic relationships in guano ecosystems are generally poorly understood and further research will undoubtedly reveal many more examples. Some of the most numerous taxa associated with guano deposits are mites (Acarina), particularly from the families Gamasidae, Actinedidae, Oribatidae and Armadillidae (Womersley 1963a, b; Gnaspini and Trajano 2000). Extremely high numbers (>33 million/m<sup>2</sup>) have been recorded on fresh guano (Harris 1973; Bellati 2001). Guanivores from all biogeographic regions are taxonomically similar, usually belonging to the same families. Differences, however, are found among the predators of guanivore communities and are often represented by taxa from different families depending on the biogeographical region (Gnaspini and Trajano 2000).

#### Bat guano micro-habitat variation

Guano environments are extremely variable, consisting of numerous micro-habitats when compared with the majority of subterranean habitats (Harris 1970). Bat guano deposits have been found to exhibit variable temperature of both the ambient air above deposits and within deposits (Harris 1970). In addition, the relative humidity, CO<sub>2</sub> concentration, and ammonia concentration also change when bats occupy a cave due to their breathing and urine (Decu 1986). Variations in pH can be extreme, resulting in strong differentiation between fresh and old guano deposits. The annual cycle of bat roosting adds a temporal component to many guano deposits and also serves to alter air temperature in roosting chambers. Bat maternal chambers are especially variable when extremely large numbers of bats enter a chamber on an annual basis to birth young (Harris 1970).

Large numbers of bats can raise the air temperature in a chamber by up to 10°C. This effect is most prevalent in high-domed chambers where heated air is trapped, but Harris (1970) also noted small increases in air temperature close to guano piles of up to 1.4°C due to heat released from guano breakdown. Increased air temperature of up to 12°C has also been noted in Cuban caves where large numbers of the leaf-nosed bat, *Phyllonycteris poeyi* Gundlach, roost (Decu 1986). This temperature increase can act as a barrier for colonisation by generalist cavernicolous invertebrate species, but allows guanophilic and guanobitic populations to reach large numbers.

Temperature within a guano pile can increase significantly with depth. Temperatures 5 cm below the surface of guano piles in Carrai Bat Cave, New South Wales are 1.7°C higher compared with surface

CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

temperatures, and 15 cm below the surface temperatures are 3.0°C higher (Harris 1970). Surface guano temperatures have also been reported to increase by 9.3°C, and these increases in both surface and subsurface temperatures were attributed by Harris (1970) to the increase in the metabolic rate of the organisms inhabiting the guano pile. The initiation of growth and reproduction of mites in guano may be linked to the increase in temperature associated with bat occupation of a chamber (Harris 1971).

Varying water content of guano due to desiccation with increasing age, results in noticeable micro-habitat differentiation. Fresh guano collected from the tops of piles in Bat Cave (U2), Naracoorte, South Australia, has been measured at up to 85% water by weight (Moulds 2003). Guano from the base of piles is a lighter grey colour due to desiccation and can contain as little as 6% water by weight (Moulds 2003). Guano moisture content increases with the birth of pups as their faecal matter is predominately liquid prior to

being weened (approximately 6-8 weeks after birth for the large bent-wing bat *Miniopterus schreibersii bassanii* Cardinal and Christidis) (T. Moulds unpublished data). The surface of guano deposits commonly exhibit a patchwork appearance of dark moist areas and light grey drier areas. Different species within guano ecosystems prefer different micro-habitats. Richards (1971) noted the majority of guanophilic arthropods in Nullarbor Plain caves were only found in completely or partially dry guano.

Guano shows a marked difference in pH between fresh and old deposits. Fresh guano is commonly basic, with the pH varying according to the volume of urine deposited with faeces. Fresh guano commonly has a pH of 8.5-9.0 that rapidly becomes acidic (5.0-5.5) with age and depth, although the centre of guano piles has a stable pH of around 4 (Harris 1971). In bat maternity caves the pH of piles will gradually decrease over winter as no fresh guano is deposited. Data from Bat Cave (U2) (Naracoorte,

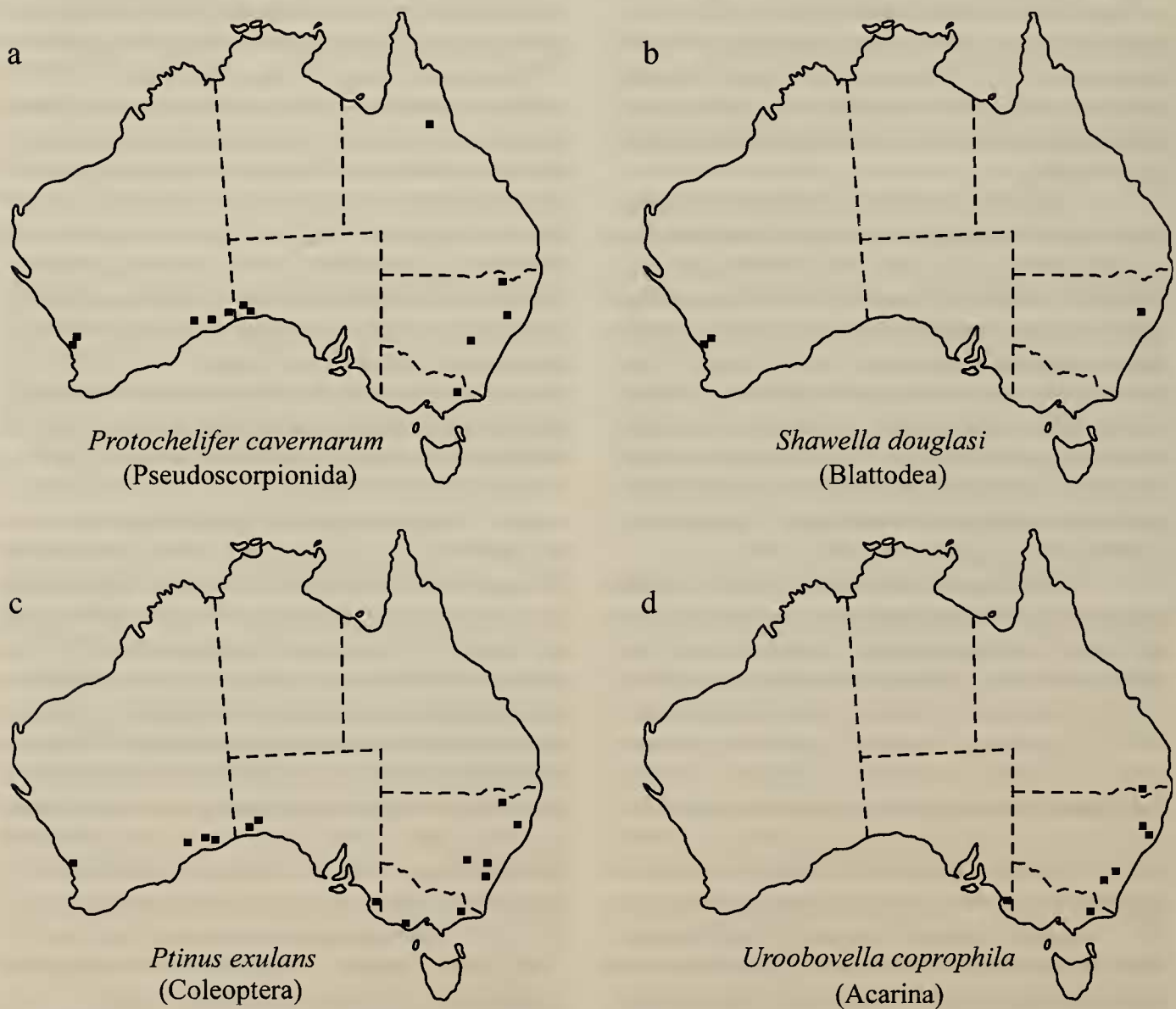


Figure 1. Different distribution patterns of guano associated species across Australia.

Table 1. Possibly endemic, guano dependent species in Australia.

State	Order	Genus and Species	Dependance		Cave
			Cave	Guano	
QLD	Pseudoscorpionida	<i>Sathrochthonius webbi</i>	Tb	Gp	Holy Jump Lava Cave (BM1)
QLD	Coleoptera	<i>Choleva australis</i>	Tp	Gp	Royal Arch Cave (CH9)
QLD	Coleoptera	<i>Dermestes uter</i>	Tp	Gp	Royal Arch Cave (CH9)
QLD	Coleoptera	<i>Alphitobius diaperinus</i>	Tp?	Gp?	Bat Cleft (E6)
QLD	Coleoptera	<i>Omorgus costatus</i>	Tp	Gp?	Johanssens Cave (J1-2)
QLD	Coleoptera	<i>Anomotarus subterraneus</i>	Tp	Gp	Riverton Main Cave (RN1)
NSW	Pseudoscorpionida	<i>Oratemnus cavernicola</i>	Tp	Gp?	Jump Up Cave, Gray Range
NSW	Pseudoscorpionida	<i>Sundochernes guanophilus</i>	Tp2	Gb	Fig Tree Cave (W148)
NSW	Pseudoscorpionida	<i>Tyrannochthonius cavicola</i>	Tp2	Gb	Grill Cave (B44)
NSW	Acarina	<i>Neotrombidium gracilipes</i>	Tp2	Gb	Fig Tree Cave (W148)
NSW	Acarina	<i>Hypoaspis annectans</i>	Tp	Gp	Carrai Bat Cave (SC5)
Nullarbor	Pseudoscorpionida	<i>Cryptocheiridium australicum</i>	Tp2	Gp	Murra-El-Elevyn Cave (N47)
Nullarbor	Isopoda	<i>Abedaioscia troglodytes</i>	Tb	Gp?	Pannikin Plain Cave (N49)
Nullarbor	Coleoptera	<i>Quedius luridipennis</i>	Tp?	Gp	Abrakurrie Cave (N3)
VIC	Pseudoscorpionida	<i>Pseudotyrannochthonius hamiltonsmithi</i>	Tp2	Gp	Mount Widderin Cave (H1)
VIC	Coleoptera	<i>Achosia lanigera</i>	Tp?	Gp	Wilson Cave (EB4)
SA	Pseudoscorpionida	<i>Austrochthonicus cavicola</i>	Tp2	Gp	Cathedral Cave (U12)
SA	Pseudoscorpionida	<i>Protochelifer naracoortensis</i>	Tp2	Gp	Bat Cave (U2)
WA	Blattodea	<i>Paratemnopteryx atra</i>	Tb	Gp	Mines nr Marble Bar
Christmas I	Coleoptera	<i>Alphitobius laevigatus</i>	Unknown	Gp	Upper Daniel Roux Cave (CI56)

South Australia), show that late in spring, before guano deposition recommences, tops of guano piles can become acidic, occasionally as low as pH 5.0 (Moulds 2003). The ever changing pH of guano piles due to age and urine content creates marked micro-habitats used by differing species.

Micro-habitat variation of bat chambers is further complicated by the movement of bat roosts in a chamber within a breeding season. These movements are a response to avoiding unfavourable conditions caused by ammonia concentrations and high local temperatures (Poulson 1972).

#### DISTRIBUTION, BIOGEOGRAPHY AND ENDEMISM

This is the first checklist for Australian guano-associated invertebrates. The full geographic range of many guanobitic and guanophilic species can now easily be appreciated. Many species have been shown to have unexpectedly wide distributions, sometimes spanning several climatic regions. Several possible explanations exist for these patterns. The lack of systematic searching and collation of published records, and collections has resulted in a poor

understanding of many species distribution and degree of endemism. This is commonly combined with a lack of accurate identification by taxonomic experts leading to the lumping of several similar species into one. Inadequate species definitions from groups requiring systematic revision will also result in species being artificially lumped or split (eg Diptera: Phoridae, David McAlpine, pers. comm. 2002). A lack of collections from most karst areas, both above and below ground, is the greatest problem, resulting in large gaps in distributions and a poor knowledge of variation within species. The paucity of records among some taxa also provides a focal point for future collecting priorities.

The collation of this checklist has revealed associations of species across wide geographic regions. Figure 1a shows the extensive range of *Protochelifer cavernarum* Beier (Pseudoscorpionida) from Jurien Bay, Western Australia, across southern Australia and north to Undara Lava Tubes in northern Queensland. The distribution of *Shawella douglasi* Princis (Blattodea: Blattellidae) (Fig. 1b) is disjunct with records from northern New South Wales and Jurien Bay, Western Australia. This may be the result of misidentification, poor taxonomic description or a paucity of collecting between these localities, especially throughout northern Australia. Despite a

number of invertebrate collections from the Nullarbor karst no individuals have been recorded, possibly due to extremely small populations of troglotic species and the extremely large size of the karst area concerned. Several species including *Ptinus exulans* Erichson (Coleoptera: Anobiidae) show very wide distributions from mid-north New South Wales across the Nullarbor Plain to the west coast of Western Australia (Fig. 1c). The distribution of *U. coprophila* (Acarina: Urodinychidae) (Fig. 1d) is directly linked to the distribution of maternal sites for the large bent-wing bat *M. schreibersii*. The single record of this species from Undara (north Queensland) may be spurious, a misidentification or an individual transported via phoresy, especially as no records exist between southern and northern Queensland despite large bat maternity caves around Rockhampton. These data raise further questions regarding the colonisation of guano deposits by invertebrates and the boundaries of possibly ill-defined species concepts.

Endemic status of guano species, has, in the past been assigned without a full understanding of the distribution of Australian guano fauna. This is apparent for the maternal chamber of Bat Cave (U2), Naracoorte, where previous studies (Hamilton-Smith 2000), identified 'several endemic species' to the maternal chamber or Bat Cave as a whole. This checklist has shown that Bat Cave contains only a single endemic species, *Protochelifer naracoortensis* Beier, and this pseudoscorpion may possibly be found in other caves in the continuous karst of the Otway Basin. Bat Cave does, however, form the most diverse guanophilic arthropod community in Australia. This highlights the amount of assumed knowledge concerning guano invertebrates in Australia and their distribution. The number of endemic species to specific bat caves is currently unknown but is almost certainly significantly lower than previously believed. Several species have been identified as possessing restricted distributions and guano dependence, although none can yet be positively identified as endemic (Table 1). The restricted distribution status of all species listed in Table 1 is tentative and more extensive collecting, both above and below ground, must be undertaken before distribution can be confirmed. This is especially true for troglitic species as epigeal occurrence of these species will effect their endemic status. The degree of a species' guano dependence will also affect its endemic status and more ecological knowledge is required to confirm species habits. Species confined to single caves or isolated areas are more likely to be endemic when combined with guano dependence. Only Fig Tree Cave (W148) (Wombeyan, NSW) and Royal Arch Cave (CH9) (Chillagoe, QLD) are found

to contain two species showing both restricted distribution and guano dependence (Table 1).

The presence of nematodes is almost a certainty in guano caves as they are almost ubiquitous in every other habitat both above and below ground. Despite this the records of nematodes from guano are extremely limited primarily because the majority of caves and karst areas remain completely unsampled for these invertebrates. Nematodes play a potentially important role in the micro-habitat of guano piles and have been recorded in large numbers from overseas caves (Decu 1986). Nematodes are also believed to be one of the first colonisers of new bat caves, being deposited by in urine and faeces (Decu 1986). Further sampling of Australian cave guano will almost certainly reveal a greater diversity of species. Currently no free living nematodes have been recorded by the author from Bat Cave, Naracoorte despite several collection events.

Currently no guano invertebrates are recorded from Tasmania, primarily due to the absence of cave-dwelling bats. The possibility remains however, that guano communities occur in orthopteran guano or other invertebrate guano deposits or even bird guano. The guanophilic mite *Macrocheles tenuirostris* Krantz and Filipponi was first recorded from mutton bird nests in Tasmania and has since been collected from bat guano in Victorian and New South Wales caves. Further field observations within Tasmanian caves may yet reveal these communities.

Opportunities for future research in this field are vast with only limited knowledge existing for most karst areas. The ecological classification for many species is poorly known and this will only be achieved through increased observations in situ. The microbiology of guano deposits also remain very poorly known in Australian, as well as in overseas caves. Many karst areas remain completely unstudied biologically, especially with regard to the diversity of invertebrate guano communities.

#### SYSTEMATIC CHECK LIST OF AUSTRALIAN GUANO INVERTEBRATES

This checklist includes all Australian cavernicolous species found in association with guano from both caves and mines. Records have been compiled from the speleological literature (both scientific and amateur), unpublished records, and personal observations. Parasites of cave-dwelling mammals (bats) have been included as they are often found in guano, although their potential roles in guano ecosystems is currently unknown. Taxa are arranged

## T. MOULDS

systematically by Phylum, Class and Order then alphabetically by Family. Undetermined taxa have been placed at the end of their respective order or family. Due to changes in taxonomy and higher systematics of many taxa the names and position of species can be uncertain. This checklist has adopted the most recent higher classifications attainable and many old names have been updated to reflect changes in the literature. Many groups in this checklist are in need of revision and so some species concepts may be altered in the future resulting in the splitting of some species and the lumping of others. This will obviously affect the distribution of species as presented in this work.

Cave names and numbers following the Australian Karst Index (Mathews 1985), and are listed for all species' records along with appropriate references. Records from caves in the Nullarbor Plain, southern Australia, have not been divided along state boundaries in order to reflect the extremely large and continuous nature of this karst area. Taxa previously considered to be obvious accidentals to cave environments have been excluded from this checklist.

The following ecological classification is modified from Hamilton-Smith (1967), and Gnaspini and Trajano (2000), and is based on the degree of cave and guano dependence of taxa. Abbreviations are those used in the checklist.

**Trogloxene (Tx):** an organism that regularly uses the cave environment for part of its lifecycle or as shelter but must leave the cave to feed and or breed.

**1<sup>st</sup> order Troglophile (Tp1):** an organism that can complete its entire lifecycle within a cave but possess

no specific adaptations to the cave environment and recorded in both epigeal and hypogean habitats.

**2<sup>nd</sup> order Troglophile (Tp2):** an organism that can complete its entire lifecycle within a cave but possess no specific adaptations to the cave environment and recorded only from hypogean habitats.

**Troglomite (Tb):** obligate cavernicolous organisms that possess specific adaptations to the cave environment.

**Guanoxene (Gx):** an organism that may use guano for reproduction and/or feeding but requires other substrates to complete its life cycle.

**Guanophile (Gp):** an organism that inhabits and reproduces both in guano piles as well as other substrates within a cave.

**Guanomite (Gb):** an organism that requires guano deposits to complete its entire life cycle.

**Bat Parasite (P):** an animal that is an obligate bat parasite requiring bats to complete its lifecycle.

Ecological classifications have been assigned to taxa wherever possible. These designations were made using available knowledge concerning behaviour, life history, and distribution within caves. However, information regarding species' ecology was found to be lacking or minimal in most cases. Because of such constraints some taxa have not been assigned a guano classification. Further, information on other taxa was insufficient to confirm their association with guano ecosystems. Thus, taxa previously recorded only from guano caves, but without a confirmed association with guano, have been included for completeness even though some of these species may be unassociated with guano.

### Phylum Platyhelminthes

#### Class Tubellaria

##### Order undetermined

Undetermined genus and species, Tx, Gx?. VICTORIA: Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

### Phylum Nematelminthes

#### Class Nematoda

##### Order Strongyloidea

###### Trichostrongylidae

*Nycteridostrogylus unicollis* Baylis, Tx, Gx, P. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data).

*Molinostrongylus dollfusi* Mawson, Tx, Gx, P. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

### Order Undetermined

#### ?Rhabditida

Undetermined genus and species, Gp?. VICTORIA: Starlight Cave (W5), Warmambool (T. Moulds unpublished data), bacterial feeder (K. Davies pers. comm. 2003).

#### Undetermined Family

Undetermined genus and species, Gp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Harris 1970).

Undetermined genus and species, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

### Phylum Mollusca

#### Class Gastropoda

### Order Stylommatophora

#### Charopidae

*Elsothera funera* Cox, Gx?. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); VICTORIA: Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

#### Undetermined Family

Undetermined genus and species, Tx, Gx?. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Carn Dum (E15), Mount Etna (Hamilton-Smith unpublished data).

### Phylum Annelida

#### Class Oligochaeta

### Order Haplotaxida

#### Lumbricidae

Undetermined genus and species, Tp, Gx?. VICTORIA: Wilson Cave (EB4), East Buchan (Yen and Milledge 1990).

### Order Undetermined

Undetermined genus and species, Tp?, Gx?. QUEENSLAND: Four Mile Cave (C14), Camooweal (Hamilton-Smith unpublished data).

### Phylum Arthropoda

#### Class Arachnida

### Order Scorpionida

#### Undetermined Family

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Order Araneae

#### Agelenidae

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

#### Amaurobiidae

Undetermined genus and species, Gx?. VICTORIA: Spring Creek Cave (B1), Buchan (Yen and



## T. MOULDS

Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Ctenizidae

*Misgolas* sp., NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Gray 1973b).

### Cyatholipidae

Undetermined genus and species, Gx?. VICTORIA: Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

### Cycloctenidae

*Cyclotenus abyssinus* Urquhart, Tp. VICTORIA: Shades of Death Cave (M3), Murrindal (Hamilton-Smith unpublished data).

*Toxopsioides* sp., Tp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b); Yessabah Bat Cave (YE1), Yessabah (Gray 1973b).

Undetermined genus and species, Gx?. VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

### Desidae

*Badumna socialis* Rainbow, Tp, Gx?. NEW SOUTH WALES: Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data).

*Colcarteria carrai* Gray, Tp?. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1992).

*Colcarteria yessabah* Gray, Tp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1992).

### Dictynidae

Undescribed genus and species, Gx?. VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Filistatidae

Undescribed genus and species, Tp2. WESTERN AUSTRALIA: Cape Range peninsula (Gray 1994).

### Gradungulidae

*Progradungula carraiensis* Forster and Gray, Tp1, Gp . NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Forster et al. 1987).

### Linyphiidae

*Laetesia weburdi* Urquhart, Gx?. NEW SOUTH WALES: Jenolan Caves (Hamilton-Smith unpublished data).

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Lycosidae

*Lycosa speciosa* Koch, Tp1. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

### Mimetidae

*Australomimetes maculosus* Rainbow, Tp. NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Gray 1973b); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); Jenolan Caves (Hamilton-Smith unpublished data).

Undetermined genus and species, Gx?. VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990).

### Pholcidae

*Physocylus* sp., NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b); Colong Main Cave (CG3), Colong (Gray 1973b).

*Psilochorus* sp., NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Gray 1973b).

### Pisauridae

Undetermined genus and species, NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Gray 1973b); Carrai Bat Cave (SC5), Stockyard Creek (Gray 1973b).

### Salticidae

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Segestriidae

Undetermined genus and species, Gx?. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Stiphidiidae

*Stiphidon* sp., Gx?. NEW SOUTH WALES: Colong Cave (CG1), Colong (Hamilton-Smith unpublished data).

### Theridiidae

*Theridon* sp., Tp, Gp. NEW SOUTH WALES: Colong Cave (CG1), Colong (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

*Steatoda* sp., Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

### Theridiosomatinae

Undetermined genus and species, Gp?. NEW SOUTH WALES: Colong Cave (CG1), Colong (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data).

### Uloboridae

*Philoponella patherinus* Keyserling, Tp. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data).

### Undetermined Family

Undetermined genus and species, Gp?. NEW SOUTH WALES: Cave C4, Comboyne (Hamilton-Smith unpublished data); The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Cave (CG1), Colong (Hamilton-Smith unpublished data); Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-

Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); Basin Cave (W4), Wombeyan (Hamilton-Smith unpublished data); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Abrakurrie Cave (N3) (Hamilton-Smith unpublished data); Madura Cave (Madura 6 Mile Cave) (N62) (Hamilton-Smith unpublished data); QUEENSLAND: Four Mile Cave (C14), Camooweal (Hamilton-Smith unpublished data); Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data); Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Piglet Help! Help! Cave (E17), Mount Etna (Hamilton-Smith unpublished data); Ilium Cave (E31), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Snowflake Cave (L1), Glenelg River (Hamilton-Smith unpublished data); Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); SSS Cave (M44), Murrindal (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Mt Widderin Cave (H1), Skipton (Hamilton-Smith unpublished data); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

### Order Opilionida

#### Triaenonychidae

*Holonuncia cavernicola* Forster, Tp2. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Hamilton-Smith 1967); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data).

*Holonuncia seriata* Roewer, Tp1, Gx. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Tp, Gp. VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990).

#### Undetermined Family

Undetermined genus and species, Tp, Gp? NEW SOUTH WALES: The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Cliefden Main Cave (CL1), Cliefden (Hamilton-Smith unpublished data); Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith unpublished data); Yessabah Bat Cave (YE1), Yessabah (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Lynch Cave (N60) (Hamilton-Smith unpublished data); QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data);

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

VICTORIA: Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Unnamed Cave (NG1), New Guinea Ridge (Hamilton-Smith unpublished data).

### Order Pseudoscorpionida

#### Atemnidae

*Oratemnus cavernicola* Beier, Tp, Gp?. NEW SOUTH WALES: Jump Up Cave, Gray Range (Beier 1976).

#### Cheiridiidae

*Cryptocheiridium australicum* Beier, Tp2, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971).

#### Cheliferidae

*Protochelifer naracoortensis* Beier, Tp2, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Beier 1968; Bellati et al. 2003).

*Protochelifer cavernarum* Beier, Tp2, Gb. NEW SOUTH WALES: Murder Cave (CL2), Cliefden (Beier 1967, 1968); Island Cave (CL6), Cliefden (Hamilton-Smith unpublished data); Belfry Cave (TR2), Timor (Beier 1967); Ashford Caves, Ashford (Beier 1968); NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Weebuddie [Weebubbie, sic] Cave (N2) (Beier 1975); Abrakurrie Cave (N3) (Richards 1971); Murrawijinie No.3 Cave (N9) (Richards 1971); Mullamullang Cave (N37) (Richards 1971); Lynch Cave (N60) (Richards 1971); QUEENSLAND: Taylor Cave (4U4), Undara (Howarth 1988); Collins Cave No.1, Undara (Howarth 1988); VICTORIA: Clogg's Cave (EB2), East Buchan (Beier 1968); WESTERN AUSTRALIA: Gooseberry Cave (J1), Jurien Bay (Beier 1968); Eneabba Caves (E1-3), Eneabba (Lowry 1996); Arramall Cave (E22), Eneabba (Lowry 1996); River Cave (E23), Eneabba (Lowry 1996); Weelawadji Cave (E24) Eneabba (Lowry 1996); Super Cave (SH1), South Hill River (Hamilton-Smith unpublished data).

*Protochelifer* sp. Tp, Gp. SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Bellati et al. 2003).

#### Chernetidae

*Sundochernes guanophilus* Beier, Tp2, Gb. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Beier 1967).

*Troglochernes imitans* Beier, Tp, Gp. NULLARBOR PLAIN: Murra-El-Elvyn Cave (N47) (Beier 1975); Cocklebidy Cave (N48) (Beier 1975); Pannikin Plain Cave (N49) (Beier 1975); Dingo Cave (Dingo-Donga) (N160) (Richards 1971).

#### Chthoniidae

*Austrochthonius cavicola* Beier, Tp, Gp. SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Beier 1968).

*Paraliochthonius cavicolus* Beier, Tp2, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

*Pseudotyranochthonius hamiltonsmithi* Beier, Tp2, Gp. VICTORIA: Mt Widderin Cave (H1), Skipton (Beier 1968).

*Sathrochthonius tuena* Chamberlin, Tp2, Gp. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Beier 1967), Deua Cave (DE1), Deua (Eberhard and Spate 1995); Punchbowl Cave (WJ8), Wee Jasper (Beier 1968); Imperial Cave (J4), Jenolan (Hamilton-Smith 1967; Gibian et al. 1988); Southern Limestone, Jenolan (Hamilton-Smith 1967; Beier 1968; Gibian et al. 1988); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data).

## T. MOULDS

*Sathrochthonius webbi* Muchmore, Tb, Gp. QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain southern Queensland (Muchmore 1982).

*Tyrannochthonius cavicola* Beier, Tp2, Gb. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Beier 1967; Harvey 1989).

### Undetermined Family

Undetermined genus and species, Tp, Gp?. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); QUEENSLAND: Royal Arch Cave (CH9), Royal Arch Tower, Chillagoe (Matts 1987).

Undetermined genus and species, Tp?, Gx. VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

## Mites

The mites have been arranged according to the higher classification used by Halliday (1998). Many changes to nomenclature have occurred since previous checklists of cavernicolous fauna have been published so the family placement of some species has been updated to reflect this. Previous family placements have not been recorded but where synonymy has occurred the old name (either family or genus) has been included in brackets. Previous generic placements have been recorded in brackets with the prefix “=”.

### Order Acariformes

#### Suborder Astigmata

##### Histiostomatidae

*Histiostoma* sp. NULLARBOR PLAIN: Mullamullang Cave (N37) (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

##### Rosensteiniidae

*Nycteriglyphus* (*Coproglyphus*) *dewae* Zakhvatkin, Tp2, Gb. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Womersley 1963a; Richards 1967b); Fig Tree Cave (W148), Wombeyan (Womersley 1963a; Richards 1967b); Railway tunnel, North Sydney (Womersley 1963a); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Womersley 1963a).

*Nycteriglyphus* sp., Tp, Gp. NULLARBOR PLAIN: Murra-EI-Elevyn Cave (N47) (Richards 1971); Dingo Cave (160) (Richards 1971).

*Glycyphagus* sp., Tp, Gp. NULLARBOR PLAIN: Murra-EI-Elevyn Cave (N47) (Richards 1971); Dingo Cave (N160) (Richards 1971).

#### Suborder Prostigmata

##### Labidostomidae

Undetermined genus and species. NEW SOUTH WALES: Island Cave (CL6), Cliefden (Hamilton-Smith unpublished data).

##### Neotrombidiidae

*Neotrombidium gracilare* Womersley, Tp2, Gb. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Womersley 1963a); Murder Cave (CL2), Cliefden (Womersley 1963a); Punchbowl Cave (WJ8), Wee Jasper (Womersley 1963a); VICTORIA: O'Rourke's Cave (B12), Buchan (Hamilton-Smith 1967); Wilson Cave (EB4), East Buchan (Hamilton-Smith 1967).

*Neotrombidium gracilipes* Womersley, Tp2, Gb. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Hamilton-Smith 1967).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

*Neotrombidium neptunium* Southcott, VICTORIA: Clogg's Cave (EB2), East Buchan (Hamilton-Smith unpublished data).

*Neotrombidium* sp., Tp, Gb. NULLARBOR PLAIN: Firestick Cave (N70) (Richards 1971); Dingo Cave (N160) (Richards 1971).

### Trombiculidae

*Rudnicula barbarae* Domrow (= *Trombicula*), Tx, Gx, P. NORTHERN TERRITORY: Kuhinoor Mine, Pine Creek (Hamilton-Smith unpublished data).

*Trombicula thomsoni* Womersley, Tx, Gx, P. NEW SOUTH WALES: Bonalbo Colliery (Hamilton-Smith unpublished data); Riverton (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Kuhinoor Mine, Pine Creek (Hamilton-Smith unpublished data).

*Trombicula dewae* Domrow, Tx, Gx, P. NORTHERN TERRITORY: Kuhinoor Mine, Pine Creek (Hamilton-Smith unpublished data).

### Order Parasitiformes

#### Suborder Ixodida

##### Argasidae

*Argas* sp., Tx, Gx, P. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

##### Ixodidae

*Amblyomma moreliae* Koch, Gx, P. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

*Ixodes simplex simplex* Neumann, Gx, P. Bat parasite in eastern Australia (Hamilton-Smith 1966b; Eberhard 1998); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); Slocombe's Cave (BA1), The Basin (Hamilton-Smith unpublished data); Anticline Cave (M11), Murrindal (Hamilton-Smith unpublished data); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

Undetermined genus and species, Gx, P. QUEENSLAND: Clam Cavern (CH26), Walkunder Tower, Chillagoe (Matts 1987); Spatial Cavern (CH41), Walkunder Tower, Chillagoe (Matts 1987); Royal Arch Cave (CH9), Royal Arch Tower, Chillagoe (Matts 1987); VICTORIA: Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data)

#### Suborder Mesostigmata

##### Ameroseiidae

*Ameroseius plumosus* Oudemans, Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

##### Laelapidae

*Cosmolaelaps* sp., Tp2, Gb. NEW SOUTH WALES: Church Cave (WJ31), Wee Jasper (Hamilton-Smith 1967); QUEENSLAND: Railway tunnel, Samford (Hamilton-Smith 1967).

*Hypoaspis (Gaeolaelaps) annectans* Womersley, Tp, Gp. NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Harris 1971).

*Hypoaspis (Gaeolaelaps)* sp.1, SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

## T. MOULDS

*Hypoaspis (Gaeolaelaps) sp.2*, SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

*Hypoaspis (Gaeolaelaps) sp.*, Tp2, Gb. NEW SOUTH WALES: Cave C4, Comboyne (Hamilton-Smith 1967).

*Ichoronyssus (Pleisiolaelaps) miniopteri* (Zumpt and Patterson 1952) (= *Neospinolaelaps*, *Spinolaelaps*), Tp, Gx, P. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998); Bonalbo Colliery (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data).

*Ichoronyssus (Pleisiolaelaps) aristippe* Domrow, NEW SOUTH WALES: Cheitmore Cave, Cheitmore (Hamilton-Smith unpublished data); Wombeyan Caves (Hamilton-Smith unpublished data); Bonalbo Colliery (Hamilton-Smith unpublished data).

### Macrochelidae

*Macrocheles spatei* Halliday, Tp1, Gp. NEW SOUTH WALES: Deua Cave (DE1), Deua National Park (Halliday 2000).

*Macrocheles tenuirostris* Krantz and Filipponi, Tp1, Gp. NEW SOUTH WALES: Paradox Cave (J48), Jenolan Caves (Halliday 2000); Cleatmore Cave, Deua National Park (Halliday 2000); Colong Cave, Woof's Cavern (CG1), Colong (Halliday 2000); Church Cave (WJ31), Wee Jasper (Halliday 2000); TASMANIA: Fisher Island, in nests and burrows of muttonbird (Krantz and Filipponi 1964); VICTORIA: Panmure Cave (H5), Warrnambool (Hamilton-Smith 1967).

### Macronyssidae

*Macronyssus aristippe* Domrow (= *Ichoronyssus*), Tp, Gx, P. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

*Trichonyssus australicus* Womersley, Tx, Gx, P. NULLARBOR PLAIN: Warbla Cave (N1) (Hamilton-Smith unpublished data).

### Parantennulidae

*Micromegistus gourlayi* Womersley. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

### Parasitidae

?*Eugamasus* sp., Tp, Gp. NULLARBOR PLAIN: Dingo Cave (N160) (Richards 1971).

### Sejidae (Ichthyostomatogastridae)

*Asternolaelaps australis* Womersley and Domrow, Tp, Gb. SOUTH AUSTRALIA: Bat Cave (U2) Naracoorte (Womersley and Domrow 1959; Hamilton-Smith 1967); VICTORIA: O'Rourke's Cave (B12), Buchan (Hamilton-Smith 1967).

### Spinturnicidae

*Spinturnix psi* Kolenati, Tp, Gx, P. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Tp, Gx, P. NEW SOUTH WALES: Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Murra-El-Elevyn Cave (N47) (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Flogged Horse Cave (Cammoo Cave) (J83), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Stockyard Cave (E3), Eneabba (Hamilton-Smith unpublished data).

### Urodynychidae

*Uroobovella (Austruropoda) coprophila* Womersley (= *Cilliba*), Tp2, Gp. NEW SOUTH WALES: Cave C4, Comboyne (Smith 1982b); Carrai Bat Cave (SC5), Stockyard Creek (Harris 1973); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data); Church Cave (WJ31), Wee Jasper (Hamilton-Smith 1966b, 1967); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith 1966b, 1967); Cheitmore Cave, Cheitmore (Hamilton-Smith unpublished data); QUEENSLAND: Arch Cave (U22), Undara (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Anticline Cave (M11), Murrindal (Hamilton-Smith 1967).

Genus and species undetermined, NEW SOUTH WALES: Deua Cave (DE1), Deua (Eberhard and Spate 1995).

### Undetermined Family

Undetermined sp. 1, Tp, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971).

Undetermined sp. 2, Tp, Gp. NULLARBOR PLAIN: Murra-El-Elevyn Cave (N47) (Richards 1971).

### Undetermined Acarina

#### Undetermined Family

Undetermined genus and species, Gp. CHRISTMAS ISLAND (Indian Ocean): Grimes Cave (CI53) (Humphreys and Eberhard 2001).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Murra-El-Elevyn Cave (N47) (Hamilton-Smith unpublished data); QUEENSLAND: Flogged Horse Cave (Cammoo Cave) (J83), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Asbestos mine near Arkaba, Flinders Ranges (Hamilton-Smith unpublished data); Drop Drop Cave (L29), Lower south east (Hamilton-Smith unpublished data); Joanna Bat Cave (U38), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); O'Rourke's Cave (B12), Buchan (Hamilton-Smith unpublished data); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

## Class Crustacea

### Order Isopoda

#### Armadillidae

*Merulana* sp. nov., Tp. NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Dennis 1986).

#### Oniscidae

*Plymphiloscia* sp. Vandel, Tp, Gp. NULLARBOR PLAIN: Pannikin Plain Cave (N49) (Richards 1971; Gray 1973a).



## T. MOULDS

Undetermined genus and species, Tp, Gp. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Carn Dum (E15), Mount Etna (Hamilton-Smith unpublished data); VICTORIA: Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data).

### Philosciidae

*Abebaioscia troglodytes* Vandel, Tb, Gp?. NULLARBOR PLAIN: Pannikin Plain Cave (N49) (Vandel 1973).

*Eurygastor montanus troglophilus* Vandel, Tp?. VICTORIA: Anticline Cave (M11), Murrindal (Vandel 1973).

*Laevophiloscia dongarrensensis* Wahrberg, Tp, Gx?. WESTERN AUSTRALIA: Yanchep Cave (YN16), Yanchep (Vandel 1973); Minnie's Grotto (YN28), Yanchep (Vandel 1973); Gooseberry Cave (J1), Jurien Bay (Vandel 1973).

*Laevophiloscia hamiltoni* Vandel, Tp, Gx. WESTERN AUSTRALIA: Weelawadji Cave (E24), Eneabba (Vandel 1973); Labyrinth Cave (AU16), Augusta (Vandel 1973)

*Laevophiloscia michaelsoni* Vandel, Tp. NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Vandel 1973).

### Porcellionidae

*Porcellio scaber* Latreille, Tp1. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

### Undetermined Family

Undetermined genus and species, Tp, Gx. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Cliefden Main Cave (CL1), Cliefden (Hamilton-Smith unpublished data); Cave C4, Comboyne (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith unpublished data); Main Cave (Ballroom Cave) (TR1), Timor (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Piano Cave (Long Cave) (WA12), Walli (Hamilton-Smith unpublished data); Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); Yessabah Bat Cave (YE1), Yessabah (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Abrakurrie Cave (N3) (Hamilton-Smith unpublished data); Cocklebiddy Cave (N48) (Hamilton-Smith unpublished data); QUEENSLAND: Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); Fox Cave (U22), Naracoorte (Hamilton-Smith unpublished data); Cave Park Cave (U37), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Drovers Cave (J2), Jurien Bay (Hamilton-Smith unpublished data); Stockyard Cave (E3), Eneabba (Hamilton-Smith unpublished data).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

### Order Amphipoda

#### Undetermined Family

Undetermined genus and species, Tp, Gx. VICTORIA: Wilson Cave (EB4), East Buchan (Yen and Milledge 1990).

### Class Myriapoda

### Order Diplopoda

#### Undetermined Family

Undetermined genus and species, Tp2, Gx. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Tp?, Gx. NEW SOUTH WALES: Island Cave (CL6), Cliefden (Hamilton-Smith unpublished data); The Drum Cave (B13), Bungonia (Hamilton-Smith unpublished data); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith unpublished data); Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Belfry Cave (TR2), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); Fig Tree Cave (W148), Wombeyan (Hamilton-Smith unpublished data); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data); Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); Yessabah Bat Cave (YE1), Yessabah (Hamilton-Smith unpublished data); QUEENSLAND: Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Piglet Help! Help! Cave (E17), Mount Etna (Hamilton-Smith unpublished data); Jolly Roger Cave (E29), Mount Etna (Hamilton-Smith unpublished data); Glen Lyon River Cave (GL1), Glen Lyon (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson Cave (EB4), East Buchan (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data).

### Order Chilopoda

#### Scolopendromorpha

Undetermined genus and species. NULLARBOR PLAIN: Mullamullang Cave (N37) (Richards 1971).

#### Undetermined Family

Undetermined genus and species, Gp?. NEW SOUTH WALES: Cave C4, Comboyne (Hamilton-Smith unpublished data); Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data); Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Moparabah Cave (MP1), Moparabah (Hamilton-Smith unpublished data); Belfry Cave (TR2), Timor (Hamilton-Smith unpublished data); NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data).

**Superclass Hexapoda**  
**Class Insecta**

**Order Collembola**

Armadillidae

*Buddelundia albomarginata* Wahrberg, Tp, Gx?. NULLARBOR PLAIN: Murrawyinee [sic] No.1 Cave (N7) (Vandel 1973); Cocklebidy Cave (N48) (Vandel 1973); Lynch Cave (N60) (Vandel 1973); Madura Cave (N62) (Vandel 1973); Old Homestead Cave (N83) (Vandel 1973); Unnamed cave (N140) (Vandel 1973).

Entomobryidae

*Lepidocyrtus* sp., Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

*Lepidosira australica* Schött, Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Undetermined genus and species, Gp?. NEW SOUTH WALES: Belfry Cave (TR2), Timor (James et al. 1976); Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data).

Hypogastruridae

*Hypogastrura* sp., NEW SOUTH WALES: Grill Cave (B44), Bungonia (Wellings 1977); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

Isotomidae

*Folsomia candida* Willem, Tp. NEW SOUTH WALES: Paradox Cave (J48), Jenolan (Eberhard 1993); Imperial Cave (J4), Jenolan (Eberhard and Spate 1995); Tuglow Main Cave (T1), Tuglow (Eberhard 1993); Jillebean Cave (Y22), Yarrangobilly (Eberhard 1993).

Paronellidae

Undetermined genus and species, NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Eberhard and Spate 1995).

Undetermined Family

Undetermined genus and species, Tp, Gp. NULLARBOR PLAIN: Cocklebidy Cave (N48) (Richards 1971); Lynch Cave (N60) (Richards 1971); Dingo Cave (N160) (Richards 1971); VICTORIA: SSS Cave (M44), Murrindal (Hamilton-Smith unpublished data); Mt Widderin Cave (H1), Skipton (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp?, Gp?. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); NORTHERN TERRITORY: 16 Mile Cave, Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Moon Cave (B2), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data).

**Order Diplura**

Undetermined family

Undetermined genus and species, SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

### Order Blattodea

#### Blattellidae

*Neotemnopteryx australis* Saussure, Tp, Gp. NEW SOUTH WALES: Moparabah Cave (Temagog Cave) (MP1), Moparabah (Hamilton-Smith 1967); Cave C4, Comboyne (Hamilton-Smith 1967); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

*Neotemnopteryx fulva* Saussure (= *Gislenia australica* Brunner), Tp, Gb. NEW SOUTH WALES: Glen Dhu Cave (Allston Cave) (TR15), Timor (Richards 1967a); Murder Cave (CL2), Cliefden (Richards 1967a); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Richards 1967a); Haystall Cave (U23), Naracoorte (Richards 1967a); VICTORIA: Mabel Cave (EB1), East Buchan (Richards 1967a).

*Neotemnopteryx* sp., Tp, Gp?. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data).

?*Neotemnopteryx* (?*Gislenia* sp.), Tp, Gp?. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Richards 1967a); Cave 4, Comboyne (Richards 1967a); Hill Cave (TR7), Timor (Richards 1967a); Moparabah Cave (Temagog Cave) (MP1), Moparabah (Richards 1967a); Swallow Cave (CU1), Cudgegong (Richards 1967a); QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Richards 1967a); Riverton Main Cave (RN1), Riverton, southern Queensland (Richards 1967a); Viator Cave (VR4), Viator Hill, southern Queensland (Richards 1967a); Johannsen's Cave (J1), Limestone Ridge, Rockhampton (Hamilton-Smith 1967); Winding Stairway Cave (4E2), Mt Etna (Hamilton-Smith 1967); SOUTH AUSTRALIA: Alexandra Cave (5U3), Naracoorte (Richards 1967a); Bat Cave (U2), Naracoorte (Richards 1967a).

*Paratemnopteryx atra* Princis, Tb, Gp. WESTERN AUSTRALIA: Mines near Marble Bar (Princis 1963; Richards 1967a; Moore et al. 2001).

*Paratemnopteryx rufa* Tepper, Gb?. NULLARBOR PLAIN: Murrawijinie No.3 Cave (N9) (Richards 1971); Abrakurrie Cave (N3) (Richards 1971).

*Paratemnopteryx* sp., Tp, Gb?. QUEENSLAND: Pinwill Cave (4U17), Undara (Howarth 1988).

*Shawella douglasi* Princis, Tp, Gb?. NEW SOUTH WALES: River Cave (SC1), Stockyard Creek (Hamilton-Smith 1967); WESTERN AUSTRALIA: Drovers Cave (J2), Jurien Bay (Hamilton-Smith unpublished data); Jurien Bay caves (Princis 1963; Richards 1967a); Eneabba Caves (E1-3), Eneabba (Lowry 1996); Weelawadji Cave (E24), Eneabba (Lowry 1996).

*Trogloblattella nullarborensis* Mackerras, Tb, Gp. NULLARBOR PLAIN: Abrakurrie Cave (N3) (Mackerras 1967; Richards 1971); Koonalda Cave (N4) (Mackerras 1967); Mullamullang Cave (N37) (Mackerras 1967); Roaches Rest Cave (N58) (Mackerras 1967); Arubiddy Cave (N81) (Mackerras 1967).

#### Blattidae

*Polyzosteria mitchelli* Angas, Tp. NULLARBOR PLAIN: Warbla Cave (N1), (Mackerras 1965); Kestrel Cavern (N40) (Mackerras 1965; Richards 1967a).

*Polyzosteria pubescens* Tepper, Tp. NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data).

## T. MOULDS

*Zonioploca medilinea* Tepper, Tp?. NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1967a).

### Order Orthoptera

#### Rhaphidophoridae

*Australotettix carraiensis* Richards, Tp, Gx. NEW SOUTH WALES: Barnett's Cave (SC6), Stockyard Creek (Richards 1964); Carrai Bat Cave (SC5), Stockyard Creek (Richards 1964); Col's Cave, Stockyard Creek (Richards 1964); Lot's Mansion, Stockyard Creek (Richards 1964); River Cave (SC1) Stockyard Creek (Richards 1964).

*Cavernotettix buchanensis* Richards, Tx, Gx. VICTORIA: Wilson Cave (EB4), East Buchan (Richards 1966; Yen and Milledge 1990); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Spring Creek Cave (B1), Buchan (Richards 1966; Yen and Milledge 1990); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa Caves (Richards 1966; Yen and Milledge 1990); Weta Cave (NN2), Nowa Nowa Caves (Richards 1966; Yen and Milledge 1990).

*Cavernotettix montanus* Richards, Tx, Gx. NEW SOUTH WALES: small cave nr Glory Cave, Yarrangobilly (Richards 1966); Jersey Cave (Y23), Yarrangobilly (Richards 1966); Restoration Cave (Y50), Yarrangobilly (Richards 1966); Unnamed cave, Yarrangobilly (Richards 1966); Cooleman Cave (CP1), Cooleman Plains (Richards 1966); Unnamed cave opp. Blue Waterhole, Cooleman Plains (Richards 1966); Unnamed cave nr Murray Cave, Cooleman Plains (Richards 1966).

*Cavernotettix wyanbenensis* Richards, Tx, Gx. NEW SOUTH WALES: Wyanbene Cave (WY1), Wyanbene (Richards 1966); Bat Cave, Cheitmore (Richards 1966).

*Pallidotettix nullarborensis* Richards, Tx, Gx. NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Weebubbie Cave (N2) (Richards 1971); Murra-El-Elevyn Cave (N47) (Richards 1971); Cocklebidy Cave (N48) (Richards 1971); Pannikin Plain Cave (N49) (Richards 1971); Tommy Grahams Cave (N56) (Richards 1971).

Undetermined genus and species, Tx, Gx. NEW SOUTH WALES: Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); QUEENSLAND: Danes Four Cave (C4), Camooweal (Hamilton-Smith unpublished data); Kaiser Creek Cave (C12) (Two Mile Cave, Tar Drum Cave), Camooweal (Hamilton-Smith unpublished data); Haunted Cave (CH1), Chillagoe (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (T. Moulds unpublished data).

### Order Psocoptera

#### Liposcelidae

*Liposcelis corrodens* Broadhead, Tp1, Gp. WESTERN AUSTRALIA: Arranmall [sic] Cave (E22), Eneabba (Smithers 1975); undetermined caves (Smithers 1975).

#### Psyllipsocidae

?*Psyllipsocus ramburi* Selys-Longcamp, Tp1, Gp. NEW SOUTH WALES: Murder Cave (CL2), Cliefden (Hamilton-Smith 1967); Island Cave (CL6), Cliefden (Smithers 1964); Hill Cave (TR7), Timor (James et al. 1976); Basin Cave (W4), Wombeyan (Smithers 1964); Fig Tree Cave (W148), Wombeyan (Smithers 1975); Punchbowl Cave (WJ8), Wee Jasper (Smithers 1964); Church Cave (WJ31), Wee Jasper (Smithers 1964); NULLARBOR PLAIN: Weebubbie Cave (N2) (Richards 1971); Abrakurrie Cave (N3) (Hamilton-Smith 1967; Richards 1971); Koonalda Cave (N4) (Richards 1971); Madura Cave (N62), (Richards 1971); QUEENSLAND: Riverton Main Cave (RN1), Riverton, southern Queensland (Hamilton-Smith 1967); SOUTH AUSTRALIA: Bat Cave

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

(U2), Naracoorte (Smithers 1964; Bellati et al. 2003); Blackberry Cave, Naracoorte (Smithers 1964); VICTORIA: Clogg's Cave (EB2), East Buchan (Smithers 1964); O'Rourke's Cave (B12), Buchan (Smithers 1964); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith 1967).

### Trogiidae

*Lepinotus inquilinus* Heyden, Tp1, Gp. WESTERN AUSTRALIA: Arranmall (sic) Cave (E22), Eneabba (Smithers 1975).

?*Lepinotus reticulatus* Enderlein, Tp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Smithers 1964; Bellati et al. 2003)

Undetermined genus and species, NEW SOUTH WALES: Fig Tree Cave (W148), Wombeyan (Dennis and Mayhew 1986).

### Undetermined Family

Undetermined genus and species, Tp, Gx. NEW SOUTH WALES: Gable Cave (CL7), Cliefden (Hamilton-Smith unpublished data); QUEENSLAND: Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); VICTORIA: Lilly Pilly Cave (M8), Murrindal (Yen and Milledge 1990).

## Order Hemiptera

### Cixiidae

Undetermined genus and species, Tp. QUEENSLAND: Mount Etna Main Cave (E1), Mount Etna (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

### Lygaeoidea

Undetermined family and genus, Gp?. VICTORIA: Starlight Cave (W5), Warrnambool (T. Moulds unpublished data).

### Reduviidae

*Armstrongula* sp. Tp, Gp. SOUTH AUSTRALIA: McKinley's Daughter's Cave (F175), Flinders Ranges (T. Moulds unpublished data); Unnamed mine, Weetootla Gorge, Gammon Ranges (T. Moulds unpublished data).

*Centrogonus* sp. Tp, Gp. NORTHERN TERRITORY: Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data).

Undetermined Emesinae genus and species, Tp, Gp. QUEENSLAND: Crazy Cracks Cave, Jacks Gorge, Broken River (T. Moulds unpublished data); Not Another Frig Tree Crave, Jacks Gorge, Broken River (T. Moulds unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Queenslander Cave (CH15), Queenslander Tower (CH5246) Chillagoe (T. Moulds unpublished data); Trezkinn Cave (CH14), Chillagoe (T. Moulds unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp?. QUEENSLAND: Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data).

## T. MOULDS

### Undetermined Family

Undetermined genus and species, QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

### Order Neuroptera

#### Myrmeleontidae

*Aeropteryx* sp., Tp, Gp. SOUTH AUSTRALIA: McKinley's Daughter's Cave (F175), Flinders Ranges (T. Moulds unpublished data); Moro Bat Cave (F47), Flinders Ranges (T. Moulds unpublished data); Unnamed cave, Brachina Gorge, Flinders Ranges (T. Moulds unpublished data); Unnamed bat cave, Chambers Gorge, Flinders Ranges (T. Moulds unpublished data); Unnamed cave, Chambers Gorge, Flinders Ranges (T. Moulds unpublished data); Unnamed mine, Weetootla Gorge, Gammon Ranges (T. Moulds unpublished data).

Myrmeleontinae sp., Tp?. QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

### Undetermined Family

Undetermined genus and species, QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data).

### Order Coleoptera

#### Anobiidae (Ptinidae)

*Ptinus exulans* Erichson, Tp1, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith 1967); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Island Cave (CL6), Cliefden (Hamilton-Smith 1967); Jenolan Caves (Hamilton-Smith 1967); Willi Willi Bat Cave (WW1), Willi Willi (Hamilton-Smith 1967); Bungonia various caves (Eberhard 1998); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Murrawijinie No. 1 Cave (N7) (Richards 1971); Murra-El-Elevyn Cave (N47) (Hamilton-Smith 1967; Richards 1971); Firestick Cave (N70) (Richards 1971); Dingo Cave (N160) (Richards 1971); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith 1967; Bellati et al. 2003); Blanche Cave (U4), Naracoorte (Hamilton-Smith 1967); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith 1967); Clogg's Cave (EB2), East Buchan (Hamilton-Smith 1967); WESTERN AUSTRALIA: Goosebury Cave (J1), Jurien Bay (Hamilton-Smith 1967).

#### Carabidae

*Anomotarus subterraneus* Moore, Tp, Gp. QUEENSLAND: Riverton Main Cave (RN1), Riverton, southern Queensland (Moore 1967).

*Cratogaster melus* Laporte, Tp?. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

*Darodilia* sp., Tp?. QUEENSLAND: Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data).

*Gnathaphanus pulcher* Dejean, Tp?. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data); Kintore Cave (K2), Katherine (Hamilton-Smith unpublished data); QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data).

*Lecanomerus* sp., Gp?. NEW SOUTH WALES: Youndales Cave (Hut Cave) (KB1), Kunderang Brook (Hamilton-Smith unpublished data).

*Mecyclothorax ambiguus* Erichson, VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

*Meonnis* sp., Tp, Gp. QUEENSLAND: Main Mount Etna Cave (E1), Mount Etna (Hamilton-Smith unpublished data).

*Mystropomus subcostatus* Chaudoir, Tp?. QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data); Piglet Help! Help! Cave (E17), Mount Etna (Hamilton-Smith unpublished data).

*Notonomus angustibasis* Sloane, Tp?, Gx. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

*Notospeophonus castaneus castaneus* Moore, Tp2. SOUTH AUSTRALIA: Blanche Cave (U4), Naracoorte (Hamilton-Smith 1967); Blackberry Cave (U8), Naracoorte (Hamilton-Smith 1967); Stick Cave (U11), Naracoorte (Moore 1964); Cathedral Cave (U12), Naracoorte (Moore 1964); Fox Cave (U22), Naracoorte (Hamilton-Smith 1967); Haystack Cave (U23), Naracoorte (Hamilton-Smith 1967); Cave Park Cave (U37), Naracoorte (Hamilton-Smith unpublished data); Tantanoola Caves (Hamilton-Smith 1967); VICTORIA: Bat Cave (P6), Portland (Moore 1962); Byaduk Caves, Byaduk (Moore 1962); Panmure Cave (H5), Mount Napier (Moore 1964); Mt Widderin Cave (H1), Skipton (Hamilton-Smith 1967); Snowflake Cave (L1), Glenelg River (Hamilton-Smith 1967); Curran's Creek Cave (G4), Glenelg River (Hamilton-Smith 1967).

*Notospeophonus castaneus consobrinus* Moore, Tp, Gp. VICTORIA: Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); Moon Cave (B2), Buchan (Hamilton-Smith unpublished data); Mabel Cave (EB1), East Buchan (Hamilton-Smith unpublished data); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Slocombe's Cave (BA1), The Basin (Hamilton-Smith unpublished data); Shades of Death Cave (M3), Murrindal (Hamilton-Smith unpublished data); Anticline Cave (M11), Murrindal (Hamilton-Smith unpublished data); SSS Cave (M44), Murrindal (Hamilton-Smith unpublished data).

*Notospeophonus jasperensis jasperensis* Moore, Tp2, Gp. NEW SOUTH WALES: Punchbowl Cave (WJ8), Wee Jasper (Moore 1964); Pylon 58 Cave (WJ99), Wee Jasper (Moore 1964); Basin Cave (W4), Wombeyan (Hamilton-Smith unpublished data).

*Notospeophonus jasperensis vicinus* Moore, Tp2, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

*Notospeophonus pallidus* Moore, Tp2, Gp?. NEW SOUTH WALES: Childrens Cave (CL12), Cliefden (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Myponga (Moore 1964); NULLARBOR PLAIN: Warbla Cave (N1) (Hamilton-Smith 1967; Richards 1971); Weebubbe Cave (N2) (Richards 1971); Abrakurrie Cave (N3) (Hamilton-Smith 1967; Richards 1971); Koonalda Cave (N4) (Hamilton-Smith 1967; Richards 1971); Koomooloobooka Cave (N6) (Richards 1971); Murrawijinie No.3 Cave (N9) (Richards 1971); Knowles Cave (N22) (Hamilton-Smith 1967; Richards 1971); Mullamullang Cave (N37) (Richards 1971); Joe's Cave (N39) (Hamilton-Smith 1967; Richards 1971); Moonera Tank Cave (N53) (Richards 1971); Madura Cave (Madura 6 Mile South Cave) (N62) (Richards 1971); Lynch Cave (N60) (Richards 1971).

*Notospeophonus* sp., Tp, Gp?. QUEENSLAND: Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data).

*Phloeocarabus* sp. Tp?, Gp?. QUEENSLAND: Haunted Cave (CH1), Chillagoe (Hamilton-Smith unpublished data).



## T. MOULDS

*Pogonoglossus* sp., Tp, Gp?. NORTHERN TERRITORY: Cutta Cutta Cave (K1), Katherine (Hamilton-Smith unpublished data).

*Pseudoceneus* sp. Tp, Gp?. WESTERN AUSTRALIA: Stockyard Cave (E3), Eneabba (Hamilton-Smith unpublished data).

*Speotarus lucifugus* Moore, Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Moore 1964; Bellati et al. 2003); NULLARBOR PLAIN: Warbla Cave (N1) (Richards 1971); Weebubbie Cave (N2) (Richards 1971); Abrakurrie Cave (N3) (Richards 1971); Koonalda Cave (N4) (Richards 1971); Winbirra Cave (N45) (Richards 1971); Murra-El-Elevyn Cave (N47) (Richards 1971); Cocklebiddy Cave (N48) (Richards 1971); Moonera Tank Cave (N53) (Richards 1971); Lynch Cave (N60) (Richards 1971); Unnamed cave (N139) (Richards 1971).

*Speotarus princeps* Moore, Tp2, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Moore 1964); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

*Speotarus* sp., Tp, Gp. NULLARBOR PLAIN: Warbla Cave (N1) (Hamilton-Smith unpublished data); Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Murra-El-Elevyn Cave (N47) (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Mount Sims Cave (F7), Walpunda Creek, Flinders Ranges (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Gooseberry Cave (J1), Jurien Bay (Hamilton-Smith unpublished data).

*Thenarotes speluncarius* Moore, Tp, Gp. NULLARBOR PLAIN: Abrakurrie Cave (N3) (Richards 1971); Koonalda Cave (N4) (Richards 1971); New Cave (N11) (Richards 1971); Lynch Cave (N60) (Richards 1971); Decoration Cave (N84) (Richards 1971); SOUTH AUSTRALIA: Cave No. 1, Buckalowie, Flinders Ranges (Hamilton-Smith unpublished data).

*Trechimorphus diemenensis* Bates, Tp1, Gx. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998); Grill Cave (B44), Bungonia (Hamilton-Smith unpublished data); Jenolan Caves (Moore 1964); VICTORIA: Dalley's Sinkhole (M35), Murrindal (Hamilton-Smith 1967).

*Trichosternus vigorsi* Gory, Tp? Gx. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

Undetermined genus and species, NEW SOUTH WALES: Grill Cave (B44), Bungonia (Eberhard and Spate 1995); Belfry Cave (TR2), Timor (James et al. 1976); Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); Tuglow Cave (T1), Tuglow (Hamilton-Smith unpublished data); QUEENSLAND: Kaiser Creek Cave (C12) (Two Mile Cave, Tar Drum Cave), Camooweal (Hamilton-Smith unpublished data); Mount Etna Main Cave (E1), Mount Etna (Hamilton-Smith unpublished data); Cave with the thing that went thump! (E5), Mount Etna (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. QUEENSLAND: Barker's Cave (U34), Undara (Hamilton-Smith unpublished data); VICTORIA: Spring Creek Cave (B1), Buchan (Yen and Milledge 1990); Mabel Cave (EB1), East Buchan (Yen and Milledge 1990); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Shades of Death Cave (M3), Murrindal (Yen and Milledge 1990); Anticline Cave (M11), Murrindal (Yen and Milledge 1990).

### Cryptophagidae

*Anchicera* sp., Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

*Atomaria* sp., Gp. Southern Australia (Hamilton-Smith 1968).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Fox Cave (U22), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data).

### Curculionidae

*Mandalotus* sp. Gp?. NEW SOUTH WALES: Chalk Cave (B26), Bungonia (Hamilton-Smith unpublished data).

*Talaurinus* sp. Gp?. QUEENSLAND: Johannsen's Cave (J1-2), Mount Etna (Hamilton-Smith unpublished data).

### Dermestidae

*Dermestes ater* DeGeer, Tp, Gp. QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); Unidentified cave in southern Queensland (Hamilton-Smith 1967); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

### Endomychidae

Undetermined genus and species, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data).

### Histeridae

*Carcinops* sp., Gp. CHRISTMAS ISLAND (Indian Ocean): Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001).

*Saprinus* sp., Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Clogg's Cave (EB2), East Buchan (Hamilton-Smith unpublished data).

*Tomogenius ?ripicola* Marseul, Tp, Gb. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Lynch Cave (N60) (Richards 1971); Thylacine Hole (N63) (Richards 1971); Dingo Cave (N160) (Richards 1971).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998); Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data); Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith unpublished data); Winding Stairway Cave (E2), Mt Etna (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Sand Cave (Joanna) (U16), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Chimney Cave (BR1), Bat Ridges, Portland (Hamilton-Smith unpublished data); Clogg's Cave (EB2), East Buchan (Hamilton-Smith unpublished data); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); WESTERN AUSTRALIA: Gooseberry Cave (J1), Jurien Bay (Hamilton-Smith unpublished data).

## T. MOULDS

### Jacobsoniidae

*Derolathrus* sp., Tp, Gb. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); Various caves in southern Australia (Hamilton-Smith 1967).

Undetermined genus and species, Tp, Gb. VICTORIA: Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data).

### Lathridiidae

*Corticaria* sp., Gp. Southern Australia (Hamilton-Smith 1968); NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith unpublished data); NULLARBOR PLAIN: Weebubbie Cave (N2) (Hamilton-Smith unpublished data); Abrakurrie Cave (N3) (Hamilton-Smith unpublished data); VICTORIA: Skipton Cave (Mount Widderin Cave) (H1), Mount Napier (Hamilton-Smith unpublished data).

### Leiodidae

*Choleva australis*, Tp, Gp. QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data).

*Choleva* sp., Tp, Gp. NULLARBOR PLAIN: Cocklebiddy Cave (N48) (Richards 1971); Lynch Cave (N60) (Richards 1971).

*Nargomorphus minusculus* Blackburn, Tp1, Gp. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Hamilton-Smith 1967; Bellati et al. 2003); VICTORIA: Anticline Cave (M11), Murrindal (Hamilton-Smith 1967).

*Pseudonemadus adelaidae* Blackburn, Tp, Gp. NEW SOUTH WALES: Glen Dhu Cave (Allston Cave) (TR15), Timor (Hamilton-Smith unpublished data); QUEENSLAND: Riverton Main Cave (RN1), Riverton (Hamilton-Smith unpublished data).

*Pseudonemadus australis* Erichson, Gp. VICTORIA: Chimney Cave (BR1), Bat Ridge, Portland (Hamilton-Smith unpublished data); Bat Cave (P6), Portland (Hamilton-Smith unpublished data); Panmure Cave (H5), Mt Napier (Hamilton-Smith unpublished data).

*Pseudonemadus integer* Portevin, Gp. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data); QUEENSLAND: Speaking Tube (E7), Mount Etna (Hamilton-Smith unpublished data); Viator Main Cave (VR1), Viator Hill (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data); VICTORIA: Trogdip Cave (EB10), East Buchan (Hamilton-Smith unpublished data); Mt Widderin Cave (H1), Skipton (Hamilton-Smith unpublished data); Panmure Cave (H5), Mt Napier (Hamilton-Smith unpublished data).

*Pseudonemadus* sp., Gp. Southern Australia (Hamilton-Smith 1968).

### ?Leiodidae

Undetermined genus and species, NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Smith 1982a).

### Melyridae

*Heteromastix* sp. Tx?, Gx?. NEW SOUTH WALES: Colong Main Cave (CG1), Colong (Hamilton-Smith unpublished data).

### Merophysiidae

Undetermined genus and species, Gp. NEW SOUTH WALES: Ashford Main Cave (AS1), Ashford (Hamilton-Smith 1967).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

### Pselaphidae

*Rybaxis?* sp., Tp, Gp. NEW SOUTH WALES: Basin Cave (W4), Wombeyan (Hamilton-Smith 1966a); Bungonia various caves (Eberhard 1998).

*Tyromorphus speciosus* King, Tp1. NEW SOUTH WALES: Unidentified cave, Southern Limestone, Jenolan (Hamilton-Smith 1966a); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data); QUEENSLAND: Johannsen's Cave (J1-2), Limestone Ridge, Rockhampton (Hamilton-Smith 1966a); VICTORIA: Anticline Cave (M11), Murrindal (Hamilton-Smith 1966a).

Undetermined genus and species, Gp. QUEENSLAND: Rope Ladder Cave, Mingella (Weinstein and Slaney 1995).

Undetermined genus and species, Tp, Gp. VICTORIA: Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data).

### Ptilidae

*Achosia lanigera* Deane, Tp?, Gp. VICTORIA: Wilsons Cave (EB4), East Buchan (Hamilton-Smith unpublished data).

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Comboyne C4 Cave, Comboyne (Hamilton-Smith unpublished data).

### Rhizophagidae

Undetermined genus and species, Gp. QUEENSLAND: Rope Ladder Cave (FR2), Mingella, Fanning River (Weinstein and Slaney 1995).

### Scarabaeidae

*Aulacopris maximus* Matthews, Tp1, Gb. NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Waite 1898); Unknown cave in Coorabakh National Park (formerly part Lansdowne State Forest), Taree (Williams 2003).

*Aulacopris reichei* White, Tp1, Gp. NEW SOUTH WALES: Yessabah Bat Cave (YE1), Yessabah (Lea 1923); Unknown cave, Mosman (Fricke 1964).

*Amphistomus accidatus* Matthews, Tx, Gp. QUEENSLAND: Elephant Hole (E8), Mount Etna (Hamilton-Smith unpublished data).

*Saprosites mendax* Blackburn, Gp. SOUTH AUSTRALIA: Cathedral Cave (U12), Naracoorte (Hamilton-Smith unpublished data).

Undetermined genus and species, Gp. NEW SOUTH WALES: Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data).

### Silphidae

*Ptomaphila lachrymosa* Schreibers, VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

### Staphylinidae

*Myotyphlus jansoni* Matthews, Tp1, Gp. NEW SOUTH WALES: Unidentified cave, Southern Limestone, Jenolan (Hamilton-Smith and Adams 1966); Paradox Cave (J48), Jenolan (Hamilton-Smith unpublished data); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith and Adams 1966); Bat Cave (P6), Portland (Hamilton-Smith 1967).

## T. MOULDS

### Tineidae

*Lindera tessellatella* Blanchard, Gb?. NEW SOUTH WALES: Humicrib Cave (WJ34), Wee Jasper (Eberhard and Spate 1995).

*Monopis crocicapitella* Clemens, Tp, Gb. NEW SOUTH WALES: Drum Cave (B13), Bungonia (Eberhard 1998); Grill Cave (B44), Bungonia (Eberhard 1998); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

*Monopis* sp., Gb. NEW SOUTH WALES: Gable Cave (CL7), Cliefden (Eberhard and Spate 1995); Colong Main Cave (CG3), Colong (Eberhard and Spate 1995); Jenolan undetermined cave (Gibian et al. 1988); Basin Cave (W4), Wombeyan (Smith 1982b); Undetermined caves, Wombeyan (Dew 1963); Signature Cave (WJ7), Wee Jasper (Hamilton-Smith unpublished data); Punchbowl Cave (WJ8), Wee Jasper (Hamilton-Smith unpublished data); Dogleg Cave (WJ10), Wee Jasper (Eberhard 1993); Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Humicrib Cave (WJ34), (Eberhard 1993); Carey's Cave (WJ100), Wee Jasper (Eberhard 1993); NULLARBOR PLAIN: Abrakurrie Cave (N3) (Richards 1971); Koonalda Cave (N4) (Richards 1971); Mullamullang Cave (N37) (Richards 1971); Cocklebiddy Cave (N48) (Richards 1971); Moonera Tank Cave (N53) (Richards 1971); Thylacine Hole (N63) (Richards 1971); Old Homestead Cave (N83) (Richards 1971); Dingo Cave (N160) (Richards 1971).

Undetermined genus and species, Gb. CHRISTMAS ISLAND (Indian Ocean): Smiths Cave (CI9) (Humphreys and Eberhard 2001); Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001); NEW SOUTH WALES: Carrai Bat Cave (SC5), Stockyard Creek (Hamilton-Smith unpublished data); Cliefden Main Cave (CL1), Cliefden (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data); QUEENSLAND: Rope Ladder Cave (FR2), Mingella, Fanning River (Weinstein and Slaney 1995); Queenslander Tower (CH5246), Chillagoe (Matts 1987); Spring Tower (CH5223-5), Chillagoe (Matts 1987); Donna Tower (CH5155), Chillagoe (Matts 1987); Royal Arch Tower (CH5158-9), Chillagoe (Matts 1987); Tea Tree Tower (CH5137), Chillagoe (Matts 1987); Ryan Imperial Tower (CH5239), Chillagoe (Matts 1987); Wallaroo Tower (CH5201), Chillagoe (Matts 1987); Tower of London Cave (CH5) Chillagoe (Matts 1987); Kaiser Creek Cave (C12) (Two Mile Cave, Tar Drum Cave), Camooweal (Hamilton-Smith unpublished data); Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data); VICTORIA: Anticline Cave (M11), Murrindal (Yen and Milledge 1990); Dickson Cave (M30), Murrindal (Yen and Milledge 1990); Nargun's Cave (NN1), Nowa Nowa (Hamilton-Smith unpublished data); Grassmere Cave (W6), Warrnambool (Hamilton-Smith unpublished data).

### Undetermined Family

Undetermined genus and species, Gp. CHRISTMAS ISLAND (Indian Ocean): Smiths Cave (CI9) (Humphreys and Eberhard 2001); Swiflet Cave (CI30) (Humphreys and Eberhard 2001); Managers Alcove (CI50) (Humphreys and Eberhard 2001); Grimes Cave (CI53) (Humphreys and Eberhard 2001); Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001).

Undetermined genus and species, NULLARBOR PLAIN: Abrakurrie Cave (N3) (Hamilton-Smith unpublished data).

## Order Hymenoptera

### Braconidae

*Apanteles ?carpatus* Say, Tp1, Gp. NEW SOUTH WALES: Humidicrib Cave (WJ34), Wee Jasper (Eberhard and Spate 1995); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

*Apanteles* sp., Tp, Gp. NEW SOUTH WALES: Church Cave (W31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (Main Cave) (WW1), Willi Willi (Hamilton-Smith unpublished data).

Undetermined genus and species. Tp?. QUEENSLAND: Holy Jump Lava Cave (BM1), Bauer's Mountain (Hamilton-Smith unpublished data).

### Formicidae

*Amblyopone australis* Erichson, VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

*Iridomyrmex purpureus* Smith, Tx, Gx. SOUTH AUSTRALIA: Eregunda Mine near Blinman, Flinders Ranges (T. Moulds unpublished data).

*Oligomyrmex* sp., Tp?, Gx?. QUEENSLAND: Crazy Cracks Cave, Jacks Gorge, Broken River (T. Moulds unpublished data).

*Pachycondyla* sp., Gp. CHRISTMAS ISLAND (Indian Ocean): Upper Daniel Roux Cave (CI56) (Humphreys and Eberhard 2001).

Undetermined genus and species, NEW SOUTH WALES: Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); QUEENSLAND: Royal Arch Cave (CH9), Chillagoe (Hamilton-Smith unpublished data); Spring Cave, Mount Surprise (Hamilton-Smith unpublished data); SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

### Ichneumonidae

Undetermined Cryptinae genus and species, Gp?. NEW SOUTH WALES: undetermined caves (Hamilton-Smith 1967); VICTORIA: Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data); Spring Creek Cave (B1), Buchan (Hamilton-Smith unpublished data); Wilson's Cave (EB4), East Buchan (Hamilton-Smith unpublished data).

### Myrmaridae

Gonatocerinae sp., Gp?. SOUTH AUSTRALIA: Bat Cave (U2), Naracoorte (Bellati et al. 2003).

### Undetermined Family

Undetermined genus and species, Tp, Gp. NEW SOUTH WALES: Bungonia various caves (Eberhard 1998).

Undetermined genus and species, Gp?. NEW SOUTH WALES: Church Cave (WJ31), Wee Jasper (Hamilton-Smith unpublished data); Willi Willi Bat Cave (WW1), Willi Willi (Hamilton-Smith unpublished data); VICTORIA: Panmure Cave (H5), Mount Napier (Hamilton-Smith unpublished data); Starlight Cave (W5), Warrnambool (Hamilton-Smith unpublished data).

## ACKNOWLEDGEMENTS

This work was only possible due to the financial support of the Department of Environment and Heritage, South Australia, and the University of Adelaide. Thanks to Stefan Eberhard and Sue White for providing the stimulus for writing this paper. Many thanks to Elery Hamilton-Smith whose critical comments and unlimited access to his personal unpublished records greatly improved this paper. Thank you to Mike Gray, Courtenay Smithers and Judy Bellati who brought additional references to my attention. I also wish to thank John Jennings and Andy Austin for editorial comments.

## REFERENCES

- Beier, M. (1967). Some Pseudoscorpionidea from Australia, chiefly from caves. *Australian Zoologist* **14**, 199-205.
- Beier, M. (1968). Some cave-dwelling Pseudoscorpionidea from Australia and New Caledonia. *Records of the South Australian Museum* **15**, 757-765.
- Beier, M. (1975). Neue Pseudoskorpione aus Australien und Neu-Guinea. *Annalen des Naturhistorischen Museums Wien* **78**, 203-213.
- Beier, M. (1976). A cavernicolous atemnid pseudoscorpion from New South Wales. *Journal of the Australian Entomological Society* **15**, 271-272.
- Bellati, J. (2001). Guanophilic invertebrate diversity and seasonality in Bat Cave at Naracoorte, South Australia. B. Sc. (Hons.). Department of Applied and Molecular Ecology, University of Adelaide, Adelaide.
- Bellati, J., Austin, A. D. and Stevens, N. B. (2003). Arthropod diversity of Bat Cave, Naracoorte Caves World Heritage Area, South Australia. *Records of the South Australian Museum, Monograph Series* **7**, 257-265.
- Calder, D. R. and Bleakney, J. S. (1965). Microarthropod ecology of a porcupine-inhabited cave in Nova Scotia. *Ecology* **46**, 895-899.
- Decu, V. (1986). Some considerations on the bat guano synusia. *Travaux Institut de Speologie "Emile Racovitza"* **25**, 41-51.
- Dennis, T. P. (1986). Specimens of amphipod and isopod observed at Wombeyan Caves, NSW, Top End Speleological Society Inc.
- Dennis, T. P. and Mayhew, B. J. (1986). Specimens of Collembola and Psocoptera observed at Wombeyan Caves, NSW, Top End Speleological Society Inc.
- Dew, B. (1963). Animal life in caves. *Australian Natural History* **15**, 158-161.
- Eberhard, S. M. (1993). Invertebrate cave fauna in NSW - Part 1, NSW Parks and Wildlife Service, 1-31.
- Eberhard, S. M. and Spate, A. (1995). Cave invertebrate survey, toward an atlas of NSW cave fauna. NSW heritage assistance program NEP 94765, 1-112.
- Eberhard, S. M. (1998). Cave invertebrates. In 'Under Bungonia'. (Eds J. Bauer and P. Bauer). Pp. 74-83, 274-279. (Alken Press, Sydney).
- Ferreira, R. L. and Martins, R. P. (1998). Diversity and distributions of spiders associated with bat guano piles in Mirrinho Cave (Bahia State, Brazil). *Diversity and Distributions* **4**, 235-241.
- Ferreira, R. L. and Martins, R. P. (1999). Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Tropical Zoology* **12**, 231-252.
- Forster, R. R., Platnick, N. I. and Gray, M. R. (1987). A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae: Araneomorphae). *Bulletin of the American Museum of Natural History* **185**, 1-116.
- Fricke, F. T. (1964). A note on *Aulacopris reichi* White (Col.: Scarabidae: Coprinae). *Journal of the Entomological Society of Australia (NSW)* **1**, 36.
- Gibian, M., Smith, G. and Wheeler, L. (1988). Interim report on the survey of the invertebrate fauna of Jenolan Caves, Jenolan Caves Reserve Trust, 8.
- Gillieson, D. (1997). 'Caves: Processes, development and management'. (Blackwell: Oxford).
- Gnaspini, P. (1992). Bat guano ecosystems. A new classification and some considerations, with special references to Neotropical data. *Mémoires de Biospéologie* **19**, 135-138.
- Gnaspini, P. and Trajano, E. (2000). Chapter 13. Guano communities in tropical caves. In 'Ecosystems of the world. Subterranean ecosystems'. (Eds H. Wilkens, D. C. Culver and W. F. Humphreys). (Elsevier: Amsterdam).
- Gray, M. R. (1973a). Cavernicolous spiders from the Nullarbor Plain and south-east Australia. *Journal of the Australian Entomological Society* **12**, 207-221.
- Gray, M. R. (1973b). Survey of the spider fauna of Australian caves. *Helictite* **11**, 47-75.
- Gray, M. R. (1992). New desid spiders (Araneae: Desidae) from New Caledonia and eastern Australia. *Records of the Australian Museum* **44**, 253-262.
- Gray, M. R. (1994). A review of filistatid spiders (Araneae: Filistatidae: Prithinae) from Australia with notes on subfamily classification. *Records of the Australian Museum* **46**.
- Halliday, R. B. (1998). 'Mites of Australia. A checklist and bibliography'. (CSIRO Publishing: Melbourne).
- Halliday, R. B. (2000). The Australian species of *Macrocheles* (Acarina: Macrochelidae). *Invertebrate Taxonomy* **14**, 273-326.
- Hamilton-Smith, E. (1966a). Pselaphidae from Australian caves. *Journal of the Entomological Society of Queensland* **5**, 70-71.

CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

- Hamilton-Smith, E. (1966b). Free-living Acarina in Australian caves. *Bulletin of the National Speleological Society* **28**, 100-103.
- Hamilton-Smith, E. and Adams, D. J. H. (1966). The alleged obligate ectoparasitism of *Myotyphlus jasoni* (Matth.) (Coleoptera Staphylinidae). *Journal of the Entomological Society of Queensland* **5**, 44-45.
- Hamilton-Smith, E. (1967). The Arthropoda of Australian caves. *Journal of the Australian Entomological Society* **6**, 103-118.
- Hamilton-Smith, E. (1968). The insect fauna of Widderin Cave, Skipton Victoria. *Victorian Naturalist* **85**, 294-296.
- Hamilton-Smith, E. (1972). The bat population of the Naracoorte caves area. *Proceedings of the 8th Conference of the Australian Speleological Society*, Australian Speleological Society.
- Hamilton-Smith, E., Holland, E. G., Mott, K. and Spate, A. (1989). Cutta Cutta Caves Nature Park draft plan of management, Conservation Commission of the Northern Territory, 18-20.
- Hamilton-Smith, E. (2000). Report on current changes in biodiversity of the Bat Cave, Naracoorte World Heritage Area., Internal report for the Department of Environment and Heritage, South Australia.
- Harris, J. A. (1970). Bat guano cave environment. *Science* **169**, 1342-1343.
- Harris, J. A. (1971). Dynamics of a bat-guano cave ecosystem with particular reference to the guano mite *Uroobovella coprophila* (Womersley). PhD Thesis. University of Queensland, Brisbane.
- Harris, J. A. (1973). Structure and dynamics of a cave population of the guano mite, *Uroobovella coprophila* (Womersley). *Australian Journal of Zoology* **21**, 239-275.
- Harvey, M. S. (1989). Two new cavernicolous chthoniids from Australia, with notes on the generic placement of the south-western Pacific species attributed to the genera *Paraliochthonius* Beier and *Morikawia* Chamberlain (Pseudoscorpionida: Chthoniidae). *Bulletin of the British Arachnological Society* **8**, 21-29.
- Hoch, H. (1988). A new cavernicolous planthopper species (Homoptera: Fulgoroidea: Cixiidae) from Mexico. *Mitteilungen der Schweizerischen entomologischen Gesellschaft* **61**, 295-302.
- Hoch, H. and Howarth, F. G. (1999). Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zoological Journal of the Linnean Society* **127**, 453-475.
- Horst, R. (1972). Bats as primary producers in an ecosystem. *Bulletin of the National Speleological Society* **34**, 49-54.
- Howarth, F. G. (1983). Ecology of cave arthropods. *Annual Review of Entomology* **28**, 365-389.
- Howarth, F. G. (1988). Environmental ecology of north Queensland caves: or why are there so many troglobites in Australia. *Proceedings of the 17th biennial Australian Speleological Federation Tropicon Conference, Lake Tinaroo, far north Queensland.*, 76-83.
- Humphreys, W. F. (1991). Experimental re-establishment of pulse-driven populations in a terrestrial troglobite community. *Journal of Animal Ecology* **60**: 609-623.
- Humphreys, W. F. and Eberhard, S. (2001). Subterranean fauna of Christmas Island, Indian Ocean. *Helictite* **37**, 59-73.
- James, J. M., Middleton, G., Montgomery, N., Parker, F., Rolls, D., Scott, P. and Wellings, G. (1976). 'Timor Caves'. (Sydney Speleological Society: Sydney).
- Krantz, G. W. and Fillipponi, A. (1964). Acari della famiglia Macrochelidae (Mesostigmata) nella collezione del South Australian Museum. *Rivista di Parassitologia* **25**, 35-54.
- Lea, A. M. (1923). Australian dung beetles of the Sub-Family Coprides. *Records of the South Australian Museum* **2**, 353-396.
- Lowry, J. W. J. (1996). Fauna found in Arramall River, Weelawadji and the Stockyard Gully Caves. <http://wasg.iinet.net.au/eneabba.html>.
- Maa, T. C. (1971). Studies in Batflies (Diptera: Streblidae: Nycteribiidae). *Pacific Insects Monographs* **28**, 1-247.
- Mackerras, M. J. (1965). Australian Blattidae (Blattodea) I. General remarks and revision of the Genus *Polyzosteria* Burmeister. *Australian Journal of Zoology* **13**, 841-882.
- Mackerras, M. J. (1967). A blind cockroach from caves in the Nullarbor Plain (Blattodea: Blattellidae). *Journal of the Australian Entomological Society* **6**, 39-44.
- Martin, B. J. (1977). The influence of patterns of guano renewal on bat guano arthropod communities, Cave Reserve Foundation. Annual Report 1976, 36-42.
- Mathews, E. G. (1986). A revision of the troglophilic genus *Brises* Pascoe, with a discussion of the Cyphaleini (Coleoptera: Tenebrionidae). *Records of the South Australian Museum* **19**, 77-90.
- Mathews, P. (1985). 'Australian Karst Index'. (Australian Speleological Federation Inc.: Sydney).
- Matts, G. (1987). History and summary of research in Chillagoe by Brother Nicholas Sullivan to end 1986. *Helictite* **25**, 74-78.
- McAlpine, D. K. (1966). Description and biology of an Australian species of Cypselosomatidae (Diptera) with a discussion of family relationships. *Australian Journal of Zoology* **14**, 673-685.
- McAlpine, D. K. (1993). A new genus of Australian cypselosomatid flies (Diptera: Nerioidae). *General and Applied Entomology* **25**, 1-4.
- Medway, L. (1962). The swiftlets (*Collocalia*) of Niah Cave, Sarawak. Part 2 Ecology and the regulation of breeding. *Ibis* **104**, 228-245.



## T. MOULDS

- Moore, B. P. (1962). Notes on Australian Carabidae III. A remarkable cave-frequenting Harpaline from Western Victoria. *Entomologist's Monthly Magazine* **97**, 188-190.
- Moore, B. P. (1964). New cavernicolous Carabidae (Coleoptera) from mainland Australia. *Journal of the Entomological Society of Queensland* **3**, 69-74.
- Moore, B. P. (1967). New Australian cave Carabidae (Coleoptera). *Proceedings of the Linnean Society of New South Wales* **91**, 179-184.
- Moore, B. P., Humphreys, W. F., Decu, V. and Juberthie, C. (2001). Australie. In 'Encyclopaedia Biospeologica'. (Eds C. Juberthie and V. Decu). (International Society of Biospeology: Moulis, France).
- Moulds, T. A. (2003). Arthropod ecology of Bat Cave, Naracoorte, South Australia. *Proceedings of the 24th Biennial Conference of the Australian Speleological Federation*, Bunbury WA, Australian Speleological Federation.
- Muchmore, W. B. (1982). A new cavernicolous *Sathrochthonius* from Australia (Pseudoscorpionida: Chthoniidae). *Pacific Insects* **24**, 156-158.
- Park, O. and Barr, T. C. J. (1961). Some observations on a cave cricket (Abstr.). *Bulletin of the Entomological Society of America* **7**, 144.
- Peck, S. B. (1976). The effect of cave entrances on the distribution of cave inhabiting terrestrial arthropods. *International Journal of Speleology* **8**, 309-321.
- Peck, S. B. and Christiansen, K. (1990). Evolution and zoogeography of the invertebrate cave faunas of the Driftless area of the Upper Mississippi River Valley of Iowa, Minnesota, Wisconsin, and Illinois, U.S.A. *Canadian Journal of Zoology* **68**, 73-88.
- Poulson, T. L. (1972). Bat guano ecosystems. *Bulletin of the National Speleological Society* **34**, 55-59.
- Princis, K. (1963). Two new Western Australian cockroaches. *Journal of the Royal Society of Western Australia* **46**, 11-12.
- Richards, A. M. (1964). The Raphidophoridae (Orthoptera) of Australia 2. A new genus. *Proceedings of the Linnean Society of New South Wales* **89**, 373-379.
- Richards, A. M. (1966). The Raphidophoridae (Orthoptera) of Australia 3. A new genus from south-eastern Australia. *Pacific Insects* **8**, 617-628.
- Richards, A. M. (1967a). Cockroaches (Blattodea) from Australian caves. *Helictite* **5**, 35-44.
- Richards, A. M. (1967b). Abstract of Free living mites (Acarina) in Australian caves. *Helictite* **5**, 70.
- Richards, A. M. (1971). An ecological study of the cavernicolous fauna of the Nullarbor Plain southern Australia. *Journal of the Zoological Society of London* **164**, 1-60.
- Smith, G. (1982a). Cave fauna. In 'Wombeyan Caves'. (Eds H. J. Dyson, R. Ellis and J. M. James). 173-178. (Sydney Speleological Society Occasional Paper)
- Smith, G. (1982b). Broad similarities in the invertebrate fauna in N.S.W. caves. *Highland Caving Group Journal* **3**, 26-30.
- Smithers, C. N. (1964). New records of cave and mine-dwelling Psocoptera in Australia. *Journal of the Entomological Society of Queensland* **3**, 85.
- Smithers, C. N. (1975). New Psocoptera records from Australian caves. *Australian Entomological Magazine* **2**, 45-46.
- Snow, D. W. (1975). Oilbirds, cave-living birds of South America. *Studies in Speleology* **2**, 257-264 +257 plates.
- Trapani, J. (1997). *Neotoma cinerea* (Bushy-Tailed Woodrat, Packrat). [http://animaldiversity.ummz.umich.edu/accounts/neotoma/n\\_cinerea.html](http://animaldiversity.ummz.umich.edu/accounts/neotoma/n_cinerea.html).
- Vandel, A. (1973). Les Isopodes terrestres de l'Australie. Etude systématique et biogéographique. *Mémoires du Muséum national d'Historie naturelle. Paris* **82**, 1-171.
- Waite, E. R. (1898). Note and exhibits. *Proceedings of the Linnean Society of New South Wales* **33**, 803.
- Weinstein, P. and Edwards, E. D. (1994). Troglophilic moths in Australia: first record of a self-sustaining population. *Journal of the Australian Entomological Society* **33**, 377-379.
- Weinstein, P. and Slaney, D. (1995). Invertebrate faunal survey of Rope Ladder Cave, Northern Queensland, a comparative study of sampling methods. *Journal of the Australian Entomological Society* **34**, 233-236.
- Wellings, G. (1977). Invertebrate fauna of Bungonia caves. In 'Bungonia Caves'. (Eds R. Ellis, L. Hawkins, R. Hawkins, J. M. James, G. Middleton, B. Nurse and G. Wellings). Pp. 150-
- Williams, G. (2003). New distribution and biological records for native dung beetles, in the tribe Scarabaeini, from northern New South Wales. *Proceedings of the Linnean Society of New South Wales* **124**, 13-16.
- Womersley, H. and Domrow, R. (1959). A new *Asternolaelaps* from Australia (Acarina: Ichthyostomatogasteridae). *Records of the South Australian Museum* **13**, 355-358.
- Womersley, H. (1963a). Two new species of Acarina from guano from Australian bat caves. *Transactions of the Royal Society of South Australia* **86**, 147-154.
- Womersley, H. (1963b). A new larval Neotrombidium (Acarina: Leeuwenhoekidae) from bat guano. *Records of the South Australian Museum* **14**, 473-476.
- Yen, A. L. and Milledge, G. A. (1990). Invertebrates of the Buchan-Murrindal area cave systems. Melbourne, Department of Conservation and Environment, Pp. 1-38.

## CAVE GUANO ECOSYSTEMS AND INVERTEBRATE CHECKLIST

Zumpt, F. and Patterson, P. M. (1952). Three new parasitic mites from the Ethiopian region (Acarina: Laelaptidae). *Journal of the Entomological Society of Southern Africa* **15**, 159-164.

# A Devonian Brachythoracid Arthrodire Skull (Placoderm Fish) from the Broken River Area, Queensland

GAVIN C. YOUNG

Department of Earth and Marine Sciences, Australian National University, Canberra ACT 0200  
gyoung@geology.anu.edu.au

Young, G.C. (2004). A Devonian brachythoracid arthrodire skull (placoderm fish) from the Broken River area, Queensland. *Proceedings of the Linnean Society of New South Wales* **125**, 43-56.

An incomplete brachythoracid arthrodire skull acid-prepared from the Devonian limestones of the Broken River area of Queensland is described as *Doseyosteus talenti* gen. et sp. nov. It supposedly comes from strata dated by conodonts as late Early Devonian in age (Emsian stage), but shows several derived features of the skull, typical of Middle-Late Devonian brachythoracids, and not seen in any arthrodire from the Emsian limestones of the Burrinjuck area of NSW. The alignment with conodont zones of stratigraphic subdivisions of the Burrinjuck sequence is revised. Published information on the provenance and age of all previously described placoderm taxa from Broken River is reviewed and amended. The new taxon may be most closely related to Late Devonian (Frasnian) brachythoracids from Iran and the Gogo Formation of Western Australia.

Manuscript received 27 May 2003, accepted for publication 22 Oct 2003.

KEYWORDS: Placoderm fishes, Arthrodira, Brachythoraci, Broken River, Devonian, new genus *Doseyosteus*, Queensland.

## INTRODUCTION

Devonian sedimentary rocks, including many marine limestones, are well exposed in the Broken River area of Queensland (Fig. 1). Conodonts form the basis for dating the sedimentary sequence (Mawson and Talent 1989; Sloan et al. 1995). Vertebrate remains reported from this sequence include microfossils from many horizons (De Pomeroy 1996; Turner, Basden and Burrow 2000), and less well known vertebrate macro-remains. The latter include two genera of antiarch placoderms described by Young (1990), a ptyctodont toothplate ascribed to *?Ptyctodus* sp. by Turner and Cook (1997), a new species of the brachythoracid arthrodire *Atlantidosteus* Lelièvre 1984 described by Young (2003a), an isolated suborbital plate of another arthrodire illustrated by Turner et al. (2000, fig. 8.7), and jaw remains of an onychodontid (Turner et al. 2000, fig. 5). Undescribed vertebrate macro-remains include various placoderm bones, most of which belong to brachythoracid arthrodires. The Arthrodira is the most diverse order within the class Placodermi, and its major subgroup, the Brachythoraci, comprises nearly 60% of about 170 genera within the Arthrodira (Carr 1995). The brachythoracid arthrodires were one of the most successful groups of early

gnathostome fishes (e.g. Young 1986; Janvier 1996). In marine environments of the Late Devonian they included probably the largest predators of their time. The major radiation of brachythoracid subgroups had apparently already occurred by the Middle Devonian, and primitive representatives were already widespread in shallow marine environments of the Early Devonian (e.g. Young et al. 2001; Mark-Kurik and Young 2003), and are important in considering the origins and interrelationships of major brachythoracid subgroups (e.g. Lelièvre 1995).

The stratigraphic occurrence of various placoderm remains in the Broken River sequence were reviewed by Young (1993, 1995, 1996), De Pomeroy (1995, 1996), and Turner et al. (2000), and they have been mentioned in relation to conodont studies by Sloan et al. (1995). There has been conflicting information published about the provenance of some of the described placoderm taxa. These were collected from the Broken River area many years ago by Professor John Jell, University of Queensland, and sent to Canberra for acid preparation and study. In this paper I describe a new arthrodire skull from this collection, and review the locality information and age determinations for previously described placoderm taxa.

DEVONIAN ARTHRODIRE SKULL FROM QUEENSLAND

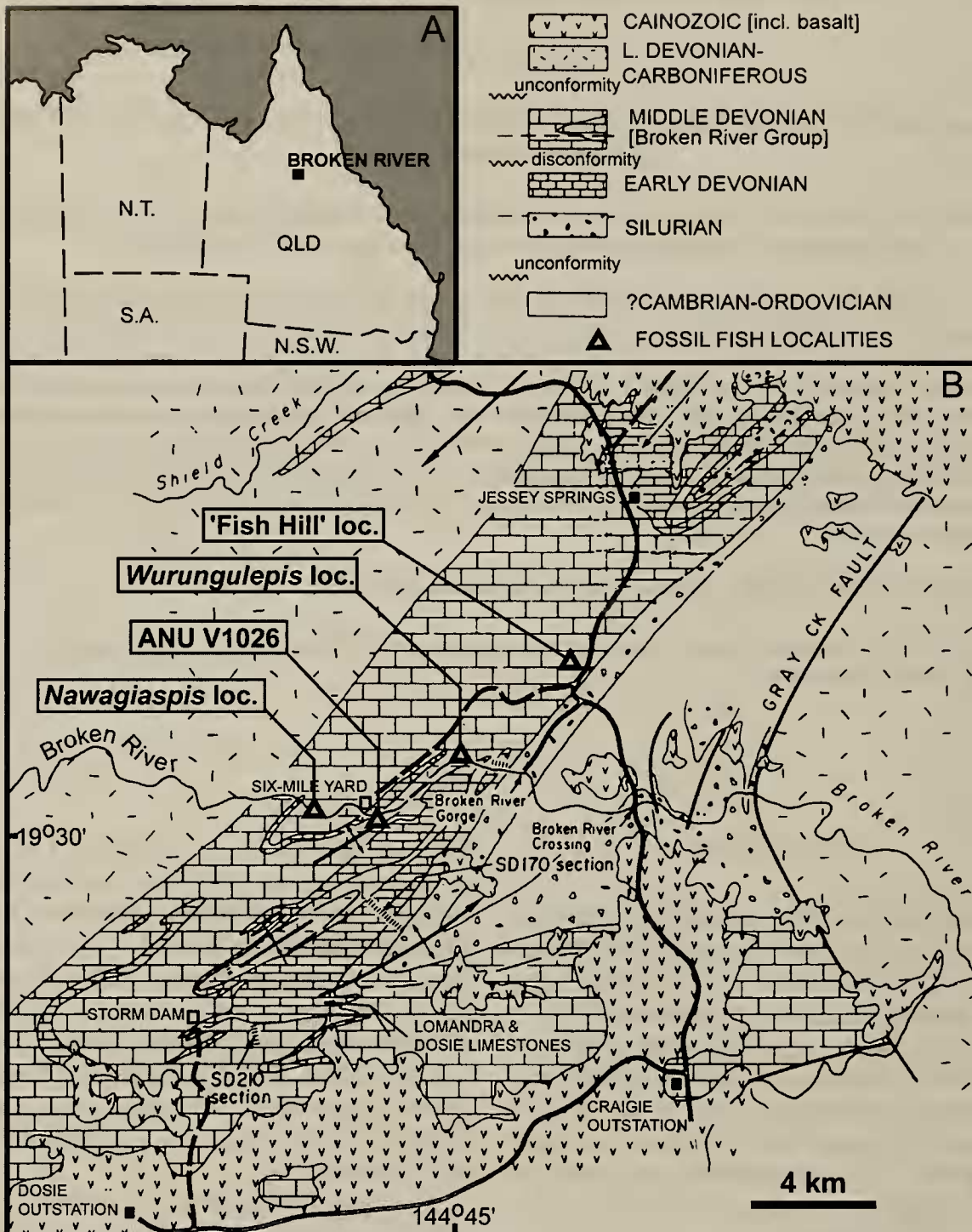


Figure 1. (A) location of the Broken River area in Queensland, Australia; (B) geological map of the collecting area (modified from Turner, Basden and Burrow 2000, fig. 2), showing localities for previously described placoderm taxa, and the specimen described in this paper (ANU V1026).

LOCALITY AND AGE OF DESCRIBED  
PLACODERM TAXA FROM THE BROKEN  
RIVER AREA

*Wurungulepis denisoni* Young 1990

According to information provided with this specimen, it came from University of Queensland

locality L4399 (not L4339, given in error by Young 1990: 45), on the north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet, and was assigned a Middle Devonian (?Eifelian) age within the Broken River Formation (J.S. Jell, letter of 17 April 1980). Judging by the map of the area

published by Sloan et al. (1995: fig. 2), the locality lies within outcrop referred to as 'undifferentiated Broken River Group'.

A 'Wurungulepis-Atlantidosteus fauna', of assumed Eifelian age, was listed in the macrovertebrate zonation of Young (1993, 1995, 1996). However De Pomeroy (1995: 480) assigned *Wurungulepis* to the late Emsian *serotinus* Conodont Zone (CZ), citing a personal communication of J.A. Talent. This information was repeated by Turner et al. (2000: 498). Later (pers. comm. 28/8/95) J.A. Talent had advised A. Basden that this specimen was collected from the grid reference cited above, situated on a bend of the Broken River in an anticline, in strata which were pre-Dosey Limestone in the sequence, and equivalent to the Bracteata Formation and Lomandra Limestone (spanning the Emsian-Eifelian boundary; Sloan et al. 1995: fig. 3).

No conodont data were obtained from the specimen, so its precise position relative to the standard conodont zonation is uncertain. *Wurungulepis* is an early representative of the asterolepidoid antiarchs, with a high short trunk armour (Young 1990), and was placed within the asterolepidoid clade adjacent to *Sherbonaspis*, and as sister group to *Stegolepis*, *Asterolepis*, *Remigolepis* and *Pambulaspis*, by Zhu (1996: fig. 29). As earlier discussed (Young 1990: 48) the initially suggested Eifelian age was consistent with the oldest asterolepid (pterichthyodid) occurrence in Europe, cited as *Gerdalepis* from the Eifelian of Germany by Denison (1978), although this occurrence is slightly younger (early Givetian) according to Otto (1998: 118). However Gardiner (1994) cited Young (1974) for an older record (Emsian) of the asterolepid antiarchs, but the 'cf. *Pterichthyodes*' mentioned by Young (1974) was based on an erroneous attribution by Hills (1958: 88) to the Early Devonian limestone sequence of an 'Antiarchan from Taemas'. In fact, the specimen in question came from the overlying Hatchery Creek Formation, of presumed Eifelian age (Fig. 2). This specimen was assigned to the new genus *Sherbonaspis* by Young and Gorter (1981). Previously, the suggested Emsian age of a pterichthyodid antiarch from the Georgina Basin (Young 1984a) was noted as possibly the oldest occurrence of this group anywhere recorded.

New evidence now indicates that two assemblages may have been mixed in this region (Burrow and Young,

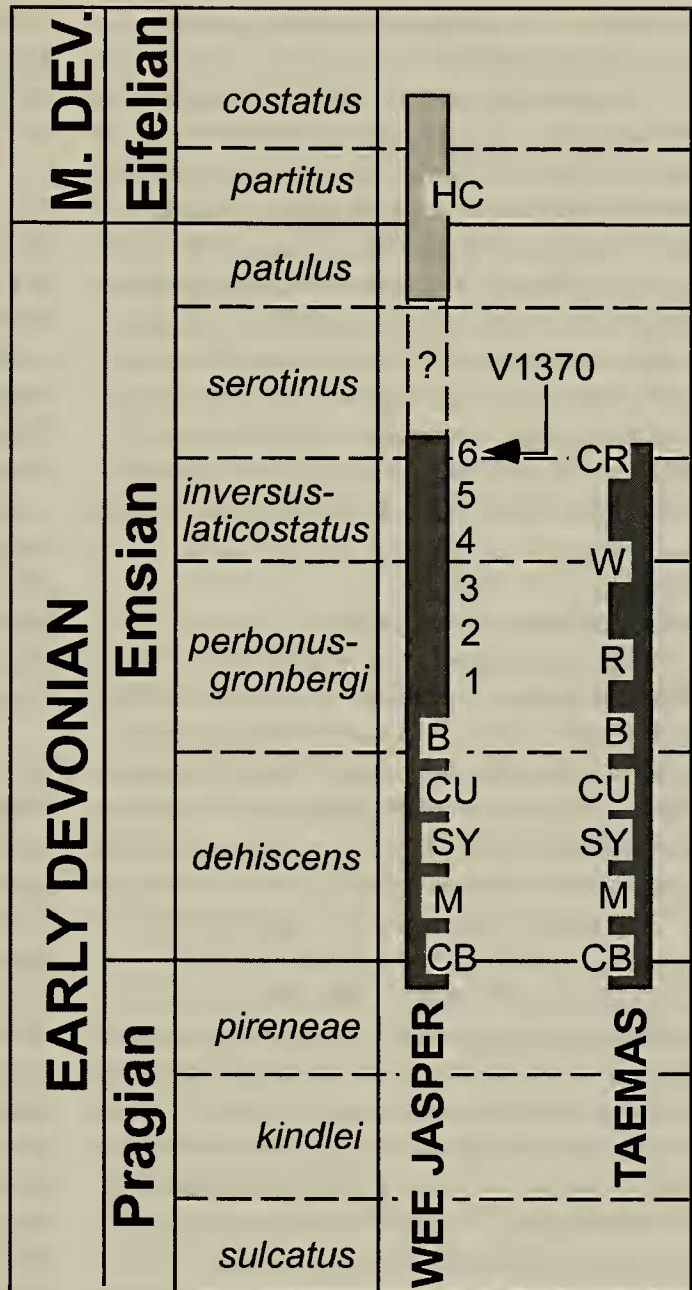


Figure 2. Proposed alignment with conodont zones of subdivisions of the Early Devonian limestone sequence (Murrumbidgee Group) around Burrinjuck Dam, N.S.W., revised from Basden et al. (2000: fig. 2). Abbreviations for stratigraphic subdivisions are: B - Bloomfield Limestone Member; CB - Cavan Formation; CR - Crinoidal Limestone Member; CU - Currajong Limestone Member; HC - Hatchery Creek Formation; M - Majurgong Formation; R - *Receptaculites* Limestone Member; SY - *Spirifer yassensis* Limestone Member; W - Warroo Limestone Member; 1-6 - units of Upper Reef Formation. V1370 - horizon for highest known arthrodire in the sequence.

in press), with the limestone occurrence yielding the antiarch probably younger than the diverse

*Wuttagoonaspis* fauna from underlying sandstones (Young and Goujet 2003).

The antiarchs are a major subgroup of the class Placodermi, ranging in age from Early Silurian to latest Devonian. In recent years there has been a significant expansion in our knowledge of the group. A cladistic analysis of their distribution in relation to phylogeny by Young (1984b) involved 22 taxa and 40 characters. In a recent review of antiarch phylogeny, Zhu (1996) noted some 45 genera and 154 species, and his data matrix used 66 characters for 40 genera. The original age assessment of Eifelian for *Wurungulepis* from Broken River is most consistent with our current knowledge of this large and diverse group.

#### *Nawagiaspis wadeae* Young 1990

This specimen is recorded from locality BRJ68D (University of Queensland locality L4428; 'small limestone outcrop on eastern side of gully 1 km upstream from Six Mile yard'), Grid Reference 596 442 on the Burges 1:100 000 sheet, which was assigned a Middle Devonian (?Givetian) age within the Broken River Formation (J.S. Jell, letter of 17 April 1980). Apparently this specimen was found by Dr Mary Wade.

Again, De Pomeroy (1995: 480) referred this taxon to the significantly older (late Emsian) *serotinus* CZ, based on its assigned position within the Bracteata Formation in section Br4 of Sloan et al. (1995, fig. 6). This information was repeated by Turner et al. (2000: 498, 506). However Prof. J.A. Talent's previous advice to the author (pers. comm. 5/8/92), was that this specimen was considerably younger (*ensensis* - *varcus* Zones; late Eifelian - Givetian). Clearly, there was some confusion about which fish specimen was being referred to. Subsequent advice given to A. Basden (pers. comm. 28/8/95), was that *N. wadeae* came from the bank of Dosey Creek (Grid Reference 616 437), the location of section Br2 within outcrop of the Bracteata Formation (Sloan et al. 1995: fig. 2). The different, and presumably correct, locality information provided with the specimen, as cited above, corresponds to the vicinity of the boundary between the Papilio and Mytton Formations on the map of Sloan et al. (1995: fig. 2). This is consistent with the Givetian age first suggested by J.S. Jell.

*Nawagiaspis wadeae* is another antiarch, originally interpreted as possibly a primitive bothriolepidoid (Young 1990), although in Zhu's (1996) phylogeny it comes out as a basal asterolepidoid. Apart from primitive Chinese antiarchs, and the erroneous Emsian pterichthyodid occurrence discussed above, the stratigraphic record of this group

is Middle-Late Devonian (Gardiner 1994, fig. 32.1). The bothriolepidoid clade had an earlier history in Asia, and apparently expanded its range to most regions of the world in the Givetian (Young 2003b).

The confusion about the provenance of this specimen may have resulted from the misconception that it was a recognisable 'skull' when collected. Turner et al. (2000) used this term to refer to the type, but the specimen as collected was a largely complete trunk armour, and the incomplete skull, missing its central portion, formed a minor part of the specimen. The whole specimen may have appeared to a non-vertebrate worker to represent a 'skull'. Such fish remains, when collected in the field, are generally not determinable until after acid preparation (e.g. the type specimen of *Atlantidosteus pacifica* Young 2003a, before preparation, was assumed to be a ventral plate of the trunk armour, rather than a large suborbital bone from the cheek).

A summary list of prepared fish remains from the original J.S. Jell collection was provided to J.A. Talent in 1995 to check on age and locality data. This list mentioned only one skull, the brachythoracid specimen described below, of which locality data provided by J.S. Jell are almost the same as stated by Sloan et al. (1995) for *N. wadeae*. Thus it seems that the specimen described below, previously listed as a 'skull', has been confused with the type of *N. wadeae*, leading to erroneous locality and age information being given in De Pomeroy (1995), Sloan et al. (1995), and Turner et al. (2000). In the context of the global distribution in time and space of this major placoderm subgroup (see above), it is almost certain that *Nawagiaspis* is Middle Devonian in age, and a Givetian age, as first suggested by J.S. Jell, is most consistent with other information about the stratigraphic distribution of the more derived antiarchs.

#### *Atlantidosteus pacifica* Young 2003a

This specimen came from locality BRJ 67B (University of Queensland locality L 4472), Grid Reference 675 485 on the Burges 1:100 000 sheet, described as 'Top of ridge to three-quarters way down western slope, west of road between Six Mile Dam and Diggers Creek' (J.S. Jell, letter of 17 April 1980). This is the locality (with a slightly different grid reference) referred to as 'Fish Hill' by Turner et al. (2000: 507). They assigned it a middle Eifelian age (*costatus* - *australis* conodont zone), but noted that Sloan et al. (1995) gave a slightly longer *partitus* - early *kockelianus* zonal range for the Fish Hill section. This is consistent with the original assignment of a Middle Devonian (?Eifelian) age within the Broken River Formation by Prof. J.S. Jell. This occurrence is

part of the evidence for proposing an Eifelian 'Wurungulepis-Atlantidosteus fauna' in the macrovertebrate zonation of Young (1993, 1995, 1996).

***Doseyosteus talenti* gen. et sp. nov.**

This specimen, described below, was the only one in the J.S. Jell collection lacking a sample number at the time of preparation. It is highly probable that it was a sample collected the year before the other material, and was taken to Canberra separately by Dr P. Jell (J.S. Jell, letter of 17 April 1980). The following locality details, provided by Prof. J.S. Jell (letter of 17 April 1980), indicate that it is the specimen collected from the alternative erroneous locality for *Nawagiaspis* just discussed: 'BRJ34 = L 4054. Grid Reference 616 438 Burges 1:100,000 sheet. Western bank of Dosey Creek, 750 m upstream from its junction with Broken River. Base of thick limestone lens in Broken River Formation, Middle Devonian. ? Eifelian'.

In a published listing of University of Queensland locality numbers (Turner et al. 2000: 506), UQL4054 is assigned to 'basal part of limestone, Lomandra/Dosey Limestone, Broken River Group', with a slightly different grid reference (615 438), but the same locality description as above. However, it is assigned to the Emsian *serotinus* CZ, citing Sloan et al. (1995).

Again, no conodonts were obtained from the sample, and section Br4 through the Bracteata Formation at this locality did not produce identifiable conodonts (Sloan et al. 1995: caption to fig. 6). Nevertheless, these authors (p.5) considered the entire formation to belong to the *serotinus* CZ, making it equivalent to the upper part of the Burrinjuck (NSW) limestone sequence, which extends from the top of the *pirenae* CZ (latest Pragian) into the *serotinus* CZ (the second youngest zone of the late Emsian). It is therefore relevant to make comparisons with the stratigraphic distribution of the diverse arthrodire assemblage described from the Burrinjuck limestone sequence.

The described arthrodire fauna from the Burrinjuck sequence (White 1952, 1978; White and Toombs 1972; Young 1979, 1981, in press a, b; Young et al. 2001; Mark-Kurik and Young 2003) includes 10 genera of brachythoracids, amongst which the most derived taxa (*Cathlesichthys* and *Dhanguura*) come from the upper part of the Wee Jasper limestone sequence. Basden et al. (2000, fig. 2) showed the youngest arthrodire skull from the Wee Jasper section (ANU V1370; the holotype of *Dhanguura*) to come from the uppermost unit 6 of the 'Upper Reef Formation' of Young (1969). This specimen is more

advanced than other arthrodires known from the Burrinjuck sequence in possessing several derived characters of the skull, the most obvious being the T-shaped rostral plate, a feature of more derived eubrachythoracids (character 5 of Carr 1991; character 4 of Lelièvre 1995). Eubrachythoracids were the most diverse fish group of the Middle and Late Devonian, and the new Broken River brachythoracid described below clearly belongs to this group, with a skull which is more advanced in several respects than any of the known Burrinjuck arthrodires (see below). Gardiner (1994) lists the first occurrence of this grouping (his family Coccosteidae) as *Coccosteus* Miller 1841 from the Middle Devonian (Eifelian) of Scotland, for which a late Eifelian age is indicated by spores of the *devonicus-naumovae* zone (V.T. Young 1995). The same species (*Coccosteus cuspidatus*) is recorded from the Kernave Member of the Narva Formation in the Baltic sequence, although a related brachythoracid '*Protitanichthys*' occurs a little earlier, and in equivalent strata (*costatus* CZ) in the Rhenish sequence (Mark-Kurik 2000). However Otto (1997: 115) suggested that remains of early eubrachythoracids (coccosteids) first occur in the early Eifelian of Scotland, Germany, and the Baltic sequence.

*Dhanguura johnstoni* Young (in press a) comes from a horizon about 420 m stratigraphically above the boundary equivalent of the Bloomfield and *Receptaculites* Members of the Taemas Limestone. A similar horizon high in the limestone sequence has produced the large lungfish *Dipnorhynchus cathlesae* Campbell and Barwick 1999. The lungfish locality is close to localities L537 and L538 of Pedder et al. (1970) which yielded tetracorals *Vepresiphyllum dumosum*, *Sulcorphyllum pavimentum*, *Chalcidophyllum vesper* and *C. gigas*. This represents the uppermost 'tetracoral teilzone' of the Murrumbidgee Group (Pedder et al. 1970: fig. 4), and is Coral Fauna F in the scheme of Garratt and Wright (1989). These authors considered the succeeding G and H Coral Faunas to overlap, and belong to the late Emsian, rather than Eifelian as previously assessed. Garratt and Wright (1989) also aligned Coral Fauna F from Wee Jasper (and the Sulcor Limestone of northern NSW) with the mid-Emsian *inversus* CZ (see column 13 of Young 1995, 1996). However Basden et al. (2000: fig. 2) showed the uppermost beds of the limestone sequence at Wee Jasper (containing Coral Fauna F) extending well into the next youngest *serotinus* CZ. Evidence supporting this (summarised by Basden 2001, table 2.1) derives from reassignment of some of the conodonts from the highest productive sample (C62) in Pedder et al.'s (1970) section 2, referred by them to *Polygnathus linguiformis*

## DEVONIAN ARTHRODIRE SKULL FROM QUEENSLAND

*linguiformis*, but reassigned to *Polygnathus inversus* by Klapper and Johnson (1975), and to *Polygnathus serotinus* (delta morphotype) by Mawson (1987). On the other hand, the age in terms of conodont zone alignment of several constituent members of the Taemas Limestone, as indicated by Basden et al. (2000, fig. 2), seem to be too young, and should be revised downwards on the following evidence. Lindley (2002a: 275) noted that the occurrence of the index species of Coral Fauna D (*Chalcidophyllum recessum*) in the Currajong Limestone Member indicates that it should be aligned with the *dehiscens* rather than the *perbonus* CZ. The overlying Bloomfield Limestone Member may also have lower beds of *dehiscens* rather than the *perbonus* CZ age (Basden 2001: table 2.1). The Warroo Limestone Member contains *perbonus* CZ elements (Nicoll, in Lindley 2002b), and the uppermost Crinoidal Limestone Member in the Taemas sequence may align with both the *inversus* and the *serotinus* CZ (Basden 2001: table 2.1).

These revised alignments are summarised in Fig. 2. Correlation with the upper part of the Wee Jasper sequence is unclear, because the constituent members of the Taemas Limestone are difficult to recognise in the thicker upper part of the sequence, represented by units 1-6 of Young (1969). If the new arthrodire skull described below from Broken River is of *serotinus* CZ age, as proposed by Sloan et al. (1995), it is still considerably more derived (see below) than any arthrodire from the Burrinjuck sequence. If correctly dated, this would indicate that derived features characterising the Middle-Late Devonian eubranchyothoracid arthrodires had originated at least by late Emsian time.

To summarise, it is emphasised that there is no overlap in the arthrodire skull characters just discussed between the Burrinjuck and Broken River limestone sequences, even though the youngest occurrences in the former sequence are also the most derived taxa within the better-documented Burrinjuck arthrodire fauna. For the new taxon described below, this evidence would support either a latest Emsian age (but younger than the Burrinjuck sequence), or an Eifelian age as originally suggested by Prof. J.S. Jell.

### ABBREVIATIONS

The specimen described below (prefix ANU V) is housed in the Earth and Marine Sciences Department, Australian National University, Canberra (GCY Vertebrate Collection). Standard abbreviations for placoderm dermal bones are used in the text and figures, and together with other morphological abbreviations are listed as follows:

**anth**, anterior nuchal thickening;  
**Ce**, central plate;  
**cf.Ce**, area overlapping Ce plate;  
**cf.M**, area overlapping marginal plate;  
**cf.PM**, area overlapping postmarginal plate;  
**cf.PtO**, area overlapping postorbital plate;  
**cr.im**, inframarginal crista;  
**csc**, central sensory line canal;  
**d.end**, openings of dermal tube for endolymphatic duct;  
**dep**, depression;  
**gr.M**, groove on Ce plate which received the edge of the marginal plate;  
**ifc.ot**, otic branch of infraorbital sensory groove;  
**if.r**, infranuchal ridge;  
**if.pt**, infranuchal pit;  
**kb**, knob-like thickening of inframarginal crista;  
**lcp**, lateral consolidated part of skull roof;  
**llc**, main lateral line sensory canal;  
**M**, marginal plate;  
**mp**, middle pitline;  
**mppr**, posterior median process of nuchal plate;  
**Nu**, nuchal plate;  
**oa.Ce**, area overlapped by Ce plate;  
**oa.M**, area overlapped by M plate;  
**oa.Nu**, area overlapped by Nu plate;  
**orb**, orbital notch;  
**Pi**, pineal plate;  
**plpr**, posterolateral process or lobe on Ce plate;  
**PM**, postmarginal plate;  
**pmc**, postmarginal sensory groove;  
**pnp**, postnuchal process of paranuchal plate;  
**PNu**, paranuchal plate;  
**pp**, posterior pitline;  
**PrO**, preorbital plate;  
**PtO**, postorbital plate;  
**R**, rostral plate;  
**soa**, subobstantic area;  
**soc**, supraorbital sensory canal;  
**th.end**, endolymphatic thickening;  
**th.pre**, pre-endolymphatic thickening;  
**tnth**, transverse nuchal ridge or thickening;  
**vg**, vascular grooves.

### SYSTEMATIC PALAEOLOGY

Class PLACODERMI McCoy, 1848  
Order ARTHRODIRA Woodward, 1891  
Suborder BRACHYTHORACI Gross, 1932

#### *Doseyosteus talenti* gen. et sp. nov.

#### Name

From Dosey Creek, the type locality, and the Greek *osteus* (bone). The species name recognises



Professor John A. Talent, Macquarie University, who has had a long and distinguished career in Devonian research, including extensive work in the Broken River area of Queensland.

### Diagnosis

A eubrachythoracid arthrodire in which the skull shows an embayed anterior margin of the nuchal plate resulting from overlap by the central plates, the central plates have strong posterolateral lobes separating the nuchal and paranuchal, and a mesial process of the marginal plate extends to the anterior angle of the paranuchal. Subobstantic area of skull extending onto marginal plate. Dermal bones smooth, or ornamented with fine tubercles.

### Remarks

Since only the skull is known, and it is incomplete, several features characterising the derived subgroup 'Eubrachythoraci' are for the present inferred for this new taxon. Definition of the eubrachythoracid arthrodires is discussed by Carr (1991: 379-381) and Long (1995: 55). Thus *Doseyosteus talenti* gen. et sp. nov. is assumed to have had a T-shaped rostral plate, a posteriorly placed pineal plate separating the preorbitals, a dermal process of the preorbital plate forming the anterodorsal margin of the orbit, and trilobate central plates. The holotype shows a strongly developed posterior thickening of the skull roof, which in the midline is represented by the anterior nuchal thickening. This is much more prominent than the transverse ridge on the posterior margin of the nuchal plate, and is a derived feature seen in coccosteomorph and pachyosteomorph brachythoracids, but generally lacking in Early Devonian taxa, for example the genus *Cathlesichthys* from Burrinjuck, NSW (Young, in press a). The embayed anterior margin and inferred proportions of the nuchal plate, and the strong posterolateral lobe of the Ce plate, are resemblances to the Late Devonian taxa *Eastmanosteus* and *Golshanichthys*, but the former differs in having the posterior pitline well developed on the posterolateral lobe of the central plate, and both forms lack the mesial process of the marginal plate inferred for this new taxon.

### Material

ANU V1026 (holotype), an incomplete skull preserved as two unconnected portions.

### Locality and Horizon

Locality BRJ34 (University of Queensland locality L4054), Grid Reference 616 438, Burges 1:100 000 sheet; western bank of Dosey Creek, 750 m

upstream from its junction with Broken River (J.S. Jell, letter of 17 April 1980; see discussion above). Horizon was described as the 'base of thick limestone lens in Broken River Formation', assigned to the Bracteata Formation (Sloan *et al.* 1995) or the 'Lomandra/Dosey Limestone, Broken River Group (Turner *et al.* 2000). Age: ?late Emsian - Eifelian (see discussion above).

### Description

ANU V1026 represents a large part of the posterolateral region of a brachythoracid skull roof, preserved as two separate portions. The larger portion (Fig. 3A,D) includes parts of the Nu, PNu and Ce plates (Fig. 4A,B), and the right postmarginal corner of the skull is preserved as a separate portion (Figs. 3B,C, 4C,D). The specimen was extracted from the rock in six pieces, but they are well preserved, suggesting that it was broken up before incorporation in the sediment. The nuchal (Nu) plate is represented by most of its right half, including the midline, so its overall shape can be estimated. Midline length of the Nu is about 70 mm. It has an embayed posterior margin, with a prominent posterior median process (mppr, Fig. 4). Except for the posterior lateral corner the right lateral margin of the Nu plate is fairly well displayed on the external surface. The bone is fractured in its middle region, and shows anteriorly that it was both overlapped and underlapped by the central (Ce) plate, a condition also reported in *Holonema* (Miles 1971). Along the anterior margin of the plate a thin overlapping lamina of the Ce plate has broken away to reveal an extensive overlap area (oa.Ce, Fig. 4B). In unbroken condition the anterior margin of the Nu plate would have been deeply embayed (Fig. 5). On its visceral surface extensive contact faces for the central plates are developed in the normal manner (cf. Ce, Fig. 4A). Other features shown are the prominent infranuchal pits (if.pt) and ridge (if.r) and the transverse nuchal thickening or ridge (tnth).

Noteworthy is the strong development of the anterior nuchal thickening (anth), which is relevant to the question of the age of this specimen (see discussion above). This is a derived feature of brachythoracids, and in ANU V1026 is more pronounced than in any Emsian brachythoracid from the Burrinjuck fauna. These have Nu plates which are fairly flat in front of the infranuchal pits. This is the case even in a form like *Cathlesichthys*, which is derived in having a very strong transverse nuchal ridge (Young in press a). In posterior view ANU V1026 shows that the anterior nuchal thickening is more pronounced than the transverse nuchal ridge, the reverse of the condition in *Cathlesichthys*. This advanced character is also seen in most Middle-Late Devonian brachythoracids, such



Figure 3. *Doseyosteus talenti* gen. et sp. nov. Holotype (ANU V1026). Larger (A,D) and smaller (B,C) skull portions in external (B,D) and internal (A,C) views.

as *Golshanichthys*, *Tafilalichthys*, and various Gogo forms (e.g. Lelièvre et al. 1981; Lelièvre 1991; Miles and Dennis 1979; Long 1988, 1995; Dennis-Bryan 1987). These taxa all resemble the giant Famennian form *Dunkleosteus*, where the 'posterior consolidated arch' of the skull roof ('PCA' of Heintz 1932: fig. 13) is a broad thickening running in front of the infranuchal pits, as the main transverse thickening of the skull. In contrast, in the Early Devonian form *Cathlesichthys* from Burrinjuck, the transverse nuchal ridge located behind the infranuchal pits forms the main thickening supporting the posterior skull margin.

The right paranuchal (PNu) plate of *Doseyosteus* gen. nov. is represented externally by an elongate portion including the mesial margin forming sutures with the Nu and Ce plates (PNu, Fig. 4B). There is also a small broken part of the postnuchal process (pnp). The PNu and Ce plates were also connected by a complex interlocking suture; a broken part around

the anterior end of the PNu exposes an overlap area (oa.Ce, Fig. 4B), and the edge of a more extensive contact face is shown on the visceral surface (cf.Ce, Fig. 4A). The endolymphatic thickening forms a broad thickened area mesially (th.end), combining with the thickened portion of the Nu plate (anth). This thickened part of the skull is much more prominent than in primitive brachythoracids like *Buchanosteus* or *Taemasosteus* (White 1978; Young 1979). Along the broken edge of the specimen, maximum bone thickness (in the part enclosing the endolymphatic duct) is almost 15 mm, which is three times the bone thickness at the anterior preserved extremity of the Nu. The exoskeletal division of the right endolymphatic duct opens on the visceral skull roof surface at the anterior edge of the area of thickened bone (th.end), and is also visible on the broken margin of the specimen (d.end, Fig.4A). This is also an advanced character of the brachythoracid skull – in large Emsian brachythoracids